THE ROLE OF OVERSTOREY PROTEOID SHRUBS IN MAINTAINING SPECIES RICHNESS IN A SOUTHERN CAPE MOUNTAIN FYNBOS COMMUNITY

by

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ABSTRACT

This study was conducted to determine if, and how, overstorey proteoid shrubs affect the species richness of a southern Cape mountain fynbos community. Protea eximia, P. lorifolia and P. repens were the dominant overstorey shrubs in the community studied.

The percentage canopy cover and density of overstorey protea shrubs before a fire were regressed against the α-diversity of understorey species after a fire, for spatial scales ranging from 1 - 100m². High canopy cover percentages (≥ 50%) and high densities (≥ 30 plants per 100m²) of overstorey proteas before a fire enriched the α-diversity levels of understorey species after a fire. The spatial scale at which α-diversity was measured affected results. The number of understorey species at a site, where overstorey proteas were absent for several fire-cycles, was compared with those where overstorey proteas persisted. The number of understorey species was least where the overstorey proteas were lacking for several fire-cycles, but results also depended on the spatial scale at which α-diversity was measured. The basal cover percentage and density of sprouting understorey species of two sites, burned at several short (6 year) fire-cycles and where overstorey proteas were lacking, were compared with those of an adjacent site which was not burned for 28 years and where the overstorey proteas persisted. Where several short fire-cycles eliminated the overstorey proteas, the basal cover percentage of understorey sprouters was approximately 32% higher than where the overstorey shrubs persisted. The number of understorey species in dense clumps of understorey sprouters was contrasted against those on 0.25m² quadrats located in the open and under burned skeletons of overstorey proteas. In dense clumps of sprouters the mean number of understorey species was less than half of that for quadrats located in the open, or for quadrats located under the burned protea skeletons. Species specific competitive interactions amongst overstorey protea and understorey sprouter species were examined for several pyric successional stages. Competitive interactions between overstorey proteas and understorey sprouters were evident in all pyric successional stages.

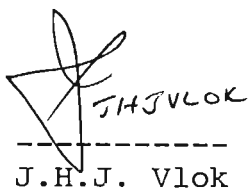
Results indicate that the overstorey proteoid shrubs are important to restrain the competitive ability of understorey sprouters, to prevent homogeneity in post-fire regeneration niches and to amplify within-community patchiness of understorey species, which ultimately enhances the species richness of fynbos communities.

PREFACE

This study was conducted under the supervision of Professor R.I. Yeaton, Department of Botany, University of Natal, Pietermaritzburg.

Data were collected during March to September 1995 from a mountain fynbos community at several study sites located in the Great Swartberg mountain range in the Oudtshoorn district of South Africa.

This study represents original work by the author and no part of it has been submitted in any form for any degree or diploma to any University. Where use of the work of others has been made it is acknowledged in the text.



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CHAPTER 1: INTRODUCTION.

1.1: The problem and study objectives

In the quest to unravel the factors which control species richness of plant communities, three components have been identified as being of paramount importance; the (i) local abiotic conditions, (ii) degree of competitive interactions amongst species and (iii) disturbance regime prevalent in the area (Tilman & Pacala 1993). Competition amongst species may limit the number of species which persist in a community, but a disturbance regime may mediate competitive interactions between species and enable a larger number of species to survive in a community (Rosenzweig 1995). Although these three factors are known to be of importance, it is not yet clear which of these factors is most important in controlling the number of species which persist in the species rich plant communities of the world. This study is an attempt to determine how competitive interactions amongst species and a local disturbance regime may affect the species richness of a mountain fynbos community.

Fynbos vegetation is one of the world's Mediterranean-type shrublands which is exceptionally rich in plant species. It is rich in species both at the point- and at the landscape-level (Taylor 1978; Kruger & Taylor 1979; Bond 1983; Cowling 1983). In previous studies on the species richness of fynbos communities the importance of abiotic factors, edaphic and climatic, received some attention (Campbell & van der Meulen

1980; Cowling 1983; Cowling *et al*, 1992). Also much attention has been given to the role which fire, the most important disturbance regime in fynbos, plays in maintaining species richness of fynbos communities (Kruger 1983; Cowling *et al* 1992; Le Maitre & Midgley 1992). Competitive interactions amongst species in fynbos communities have, however, rarely been studied. A lone example is that by Yeaton & Bond (1991), who have shown that the persistence of species in fynbos communities depends on their life history traits, with the outcome of competitive interactions between species affected by the prevalent fire regimes.

The regeneration success of individual species or guilds of fynbos species after fire have often been studied (Bond *et al* 1983; Le Maitre & Midgley 1992). These studies provided valuable information on how certain guilds of species would fare under different fire regimes. However, these studies did not help much to resolve the uncertainty that a fire regime, which would enable one guild of species to persist, would also enable other guilds of species to persist (Cowling & Gxaba 1990; Keith & Bradstock 1994; Van Wilgen *et al* 1994). As species richness tends to reach its maximum at intermediate disturbance regimes in most biological communities (Huston 1979; Rosenzweig 1995), a general recommendation for fynbos vegetation has been an intermediate fire regime (Cowling *et al* 1992). However, what exactly the ideal intermediate fire regime is, is not known for the fynbos or other fire-driven vegetation

types (Collins *et al* 1995; Bond & Van Wilgen 1996). Uncertainty still exists as to whether there is an ideal intermediate fire regime which would facilitate a maximum number of species to persist in Mediterranean-type shrubland communities. Part of the problem of defining an intermediate fire regime, lies in the fact that a fire regime has at least three distinct variables; (i) frequency of fires, (ii) season of fire and (iii) intensity of fire (Bond & Van Wilgen 1996). As three variables are involved, it is not possible to determine a single fire regime which is intermediate in all three aspects. Much of the debate about the most desirable intermediate fire regimes can be resolved, if we consider the role which a disturbance (fire) regime plays in the maintenance of the species richness of communities. Periodic disturbances can mediate competitive interactions amongst organisms, which may prevent competitive displacement of species from a community (Rosenzweig 1995 and references therein). Unfortunately little is known about competitive interactions between different guilds of species in Mediterranean-type shrublands and, in particular, how the outcome of such competitive interactions may be affected by different fire regimes.

One of the most prominent and best studied guilds of species in fynbos are the overstorey proteoid shrubs. In many mountain fynbos communities the overstorey canopy is dominated by tall shrubs which belong to the family, Proteaceae (Campbell 1985). This is also the case in the community studied (Figure

1.1). Most of these overstorey proteoid shrubs are usually slow to mature after a fire. They need fire to recruit as their seeds are stored in serotinous cones. These shrubs become

FIGURE 1.1: A 16-year old mountain fynbos community on the upper northern slopes of the Swartberg mountain range. The red-flowered shrub on the left is *Protea repens* and grey-leaved shrub on the right, *Protea lorifolia*. Note the variability in density of the proteoid shrubs in the foreground and on the hillside.

moribund if not burned for several decades (Bond 1980). The age to maturity and longevity of these shrubs is often used to determine fire frequencies for fynbos communities (Kruger 1983). As these shrubs tend to be the slowest to mature after a

fire, the argument for using them as indicator species to determine fire regimes has been that fire regimes, which would allow these overstorey shrubs to persist, would also allow all other species in fynbos communities to complete their life cycles. This argument has, however, been criticized, particularly as high densities of these overstorey proteoid shrubs may displace understorey species (Cowling & Gxaba 1990; Esler & Cowling 1990; Keith & Bradstock 1994).

A general model to explain patterns in the species richness of shrublands of temperate climates has been developed (Specht & Morgan 1981; Specht & Specht 1989). Assumptions of this model are that (i) understorey species richness is reduced by high overstorey densities, (ii) understorey species tend to contribute more to community richness than overstorey species, and (iii) areas with high plant productivity support a better developed overstorey canopy. With these assumptions this model predicts that communities which occur in areas where high plant productivity can be supported, will have lower species richness than communities which occur at sites where low plant productivity is sustained. However, this model is not compatible with data available for the fynbos. For example, Bond (1983) showed that the species richness of fynbos communities is sigmoidally related to plant productivity. This relationship has also been observed in many other vegetation types (Tilman & Pacala 1993).

Pyric successional phases can explain how many species manage to persist in fynbos communities. The species richness of fynbos communities is highest soon after a fire because all species regenerate in the post-fire environment, either as seedlings of non-sprouting species, or as resprouts from mature plants of sprouting species. As the fynbos vegetation ages, α-diversity levels decline, with short-lived species gradually being displaced by longer-lived species. Although some species may be displaced during an inter-fire period, they may persist as soil stored propagules and re-appear after the following fire (Kruger 1983; Kruger & Bigalke 1984). Displacement of species may thus only be temporal, with different guilds of species exploiting different pyric successional stages to complete their life-cycles. When recording α-diversity values of fynbos communities, care should be taken to do so soon after a fire, as pyric successional patterns may affect results. Many species may thus be able to coexist in fynbos communities, as competitive displacement may be restricted only to the regeneration phase immediately after a fire.

At least one guild of species may have a competitive advantage over other species in the post-fire environment. Species which are able to resprout after a fire (hereafter referred to as sprouters) may have a competitive advantage over other species. After a fire they are able to re-establish quickly from their vegetative storage organs, whilst non-sprouting species tend to be slow to mature (Bell *et al* 1987).

The competitive effect of sprouters is quite obvious (Figure 1.2), but not yet investigated in fynbos communities. Sprouting species may be favoured under fire regimes of several short fire-cycles, as they will have several post-fire events in which they may gain a competitive advantage over other species. Under such fire regimes sprouters may thus increase in density and become dominant (Kruger 1983; Kruger & Bigalke 1984).

FIGURE 1.2: Effect of competition from understorey sprouters on the performance of the overstorey shrub *Protea lorifolia*. Both plants are 12-years old, but the taller plant on the right escaped competition because it germinated in the open, whilst the plant on the left suffered from competition because it established in a tussock of understorey sprouters.

Before the effect of different fire regimes on species richness of fynbos communities can be predicted, we need to know (i) how high canopy densities of overstorey species affect the number of understorey species; (ii) how high basal covers of understorey sprouters affect the number of understorey species and (iii) how competitive interactions amongst non-sprouting overstorey and sprouting understorey species are affected by different fire-cycles. To answer these questions I studied the interactions between overstorey and understorey species in a southern Cape mountain fynbos community. The following specific questions are addressed in this study;

(a) Does the pre-fire density of overstorey shrubs affect the post-fire α-diversity levels of a fynbos community? (Chapter 2)

(b) Does the recurrent absence of an overstorey of proteoid shrubs, over several fire-cycles, affect α-diversity levels? (Chapter 2)

(c) Do resprouting understorey species increase in density when overstorey shrubs are absent for several fire-cycles? (Chapter 3)

(d) Do high densities of resprouting understorey species affect α-diversity levels of fynbos communities? (Chapter 4)

(e) Are there competitive interactions between non-sprouting overstorey shrubs and resprouting understorey species? (Chapter 5)

1.2 Study area and material

1.2.1 Study area

The study area is approximately 30.0 km long and 2.5 km wide and is located on the upper, northern slopes of the Great Swartberg mountain range in the Oudtshoorn district of South Africa (Figure 1.3). Seven subsidiary study sites were used in the study area. These study sites were not numbered sequentially in an east-west direction, but chronologically as the data collected from these are reported in each chapter. The location, altitude, aspect and fire history of the study sites are briefly summarized in Table 1.1. As the fire history of a site is of particular relevance in this study, it will be described in more detail for each site in each chapter.

The rainfall of the study area shows a weakly bimodal pattern with spring and autumn peaks (Bond 1980; Cowling & Holmes 1992). Both annual precipitation and air temperatures are strongly affected by altitude and aspect in the study area (Schulze 1965; Bond 1981). To ensure that the micro-climates of study sites are similar, the sites were located in a similar topographical position (on upper north-facing aspect of mountain), on gentle north-facing slopes (3-5°), with a relatively small difference in altitudinal range (200 m). Exact rainfall data are not available for each study site, but annual rainfall could be estimated from two rain gauges located in the

TABLE 1.1: Location and fire history of study sites. (Fire histories were determined from unpublished records of the Swartberg Nature Reserve).

SITE 1

Location: 33°19'15" S 22°14'30" E
Altitude: 1500 m Aspect: NNE-NNW
Fire History: Date of last fire; November 1993
Age of vegetation with last fire; 13 years
Preceding fire frequency; 13 years

SITE 2

Location: 33°21'00" S 21°57'50" E
Altitude: 1400 m Aspect: N
Fire History: Date of last fire; March 1986
Age of vegetation with last fire; 8-28 years
Preceding fire frequency; Complex see Fig. 2.1

SITE 3

Location: 33°20'50" S 22°03'15" E
Altitude: 1350 m Aspect: NNE
Fire History: Date of last fire; February 1992
Age of vegetation with last fire; 13 years
Preceding fire frequency; 12 years

SITE 4

Location: 33°20'50" S 22°00'30" E
Altitude: 1350 m Aspect: N
Fire History: Date of last fire; May 1980
Age of vegetation with last fire; 10 years
Preceding fire frequency; 11 years

SITE 5

Location: 33°21'00" S 21°58'20" E
Altitude: 1350 m Aspect: NNE
Fire History: Date of last fire; January 1980
Age of vegetation with last fire; 20 years
Preceding fire frequency; 19 years

SITE 6

Location: 33°20'05" S 22°02'05" E
Altitude: 1350 m Aspect: N
Fire History: Date of last fire; February 1992
Age of vegetation with last fire; 17 years
Preceding fire frequency; 16 years

SITE 7

Location: 33°21'10" S 21°57'00" E
Altitude: 1300 m Aspect: NNE
Fire History: Date of last fire; November 1987
Age of vegetation with last fire: 21 years
Preceding fire frequency; 6 years

study area. During the study period, 1995, the total annual rainfall at both these rain guages was 720 mm, which is well within the 600 - 800 mm annual rainfall range recorded for the 1980-1990 period (determined from Tolhuis & Dewetsvlei rain gauges of the Swartberg Nature Reserve; Cape Nature Conservation, unpublished records).

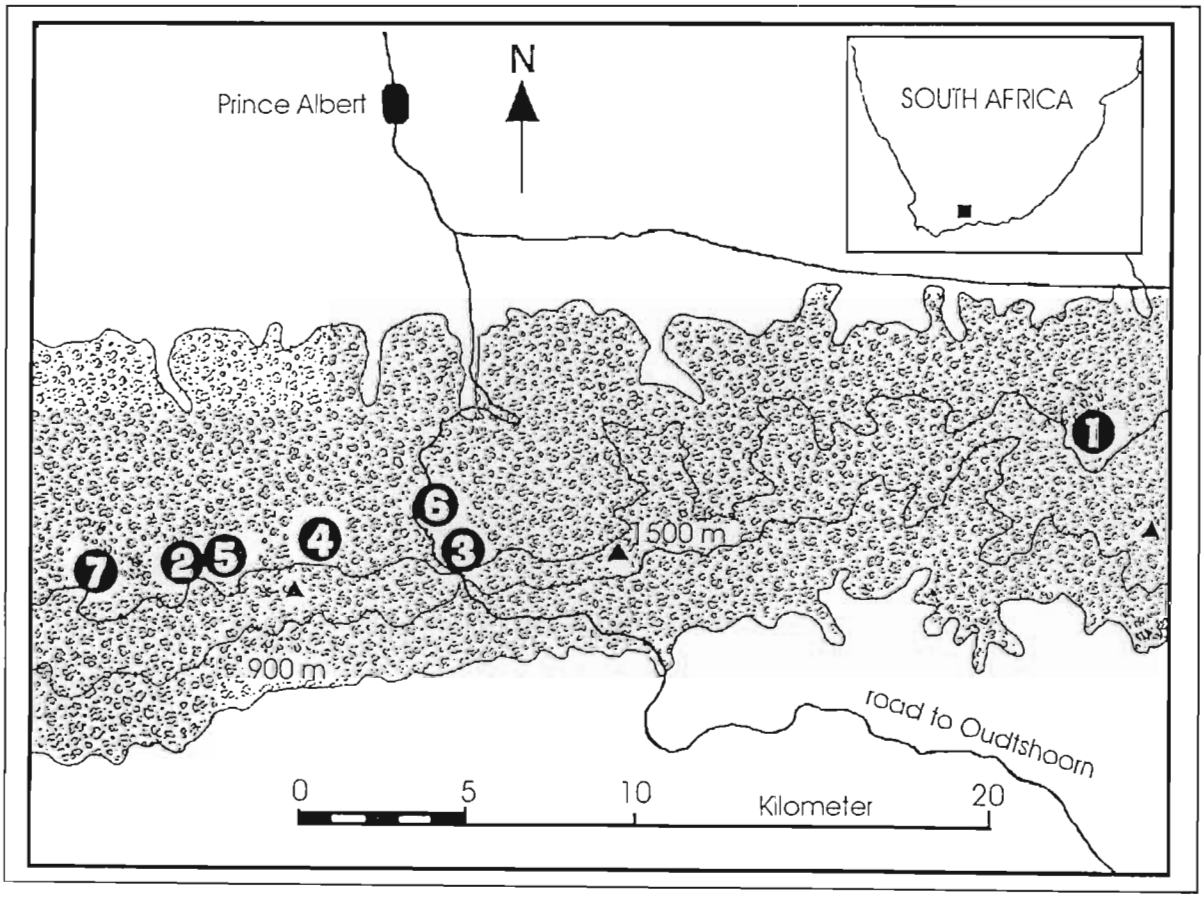

FIGURE 1.3: Location of the study area. Numbered solid circles indicate the location of the seven study sites. The lower altitudinal line (900 m altitude) indicate the outline of the Swartberg mountain and upper altitudinal line indicate 1500 m altitude. Solid triangles indicate trigonometric beacons on prominent mountain peaks.

The underlying geology of the study area consists of quartzitic sandstone, generally known as Table Mountain Sandstone, but presently referred to as Table Mountain Group of the Cape Supergroup (Theron 1983). Soils derived from these quartzitic sandstones are lithosols, which are nutrient poor, shallow, acidic and sandy soils (Campbell 1983; Deacon *et al* 1992). Shale bands derived from a different geology (Bokkeveld Group), also occur in the study area. Study sites were carefully selected to exclude these shales, as such soils differ in texture and nutrient status to those derived from sandstone (Bond 1981). Care was also taken to ensure that water availability and drainage of study sites are similar, by means of only selecting sites situated on gentle slopes where no water streams or seepage areas occurred. Apart from small differences in soil depth (0.2 - 0.6 m), steepness of slope (3 - 5°) and percentage surface rock cover (5 - 25%), no differences in edaphic or other micro-climatic factors could be detected between the seven study sites.

Mesic Mountain Fynbos is the dominant vegetation type in the study area (Moll *et al* 1984). In fynbos communities three main structural classes can be recognized; (i) an overstorey of broad-leaved proteoid shrubs, (ii) an intermediate layer of small-leaved ericoid shrubs and (iii) an understorey of graminoid/restioid tussocks (Taylor 1978). At all seven study sites, the species most abundant in each of these three structural classes were similar. Only one comparable mountain

fynbos community was therefore sampled at the seven study sites. The species which were most abundant in each of the structural classes were: (i) *Protea eximia*, *Protea repens* and *Protea lorifolia* as proteoid shrubs; (ii) *Agathosma capensis*, *Aspalathus rubens*, *Lightfootia rubens*, *Metalasia massonii*, *Selago albida*, *Syncarpha paniculata* and *Thesium carinatum* as ericoid shrubs and (iii) *Cannamois scirpoides*, *Hypodiscus albo-aristatus*, *Hypodiscus striatus*, *Pentameris distichophylla*, *Pentaschistis pallida*, *Restio triticeus*, *Rhodocoma fruticosa*, *Tetraria ustulata*, *Thamnochortus rigidus* and *Willdenowia teres* as graminoid/restioid elements (nomenclature of species follows Bond & Goldblatt 1984 throughout this dissertation). The floristic and structural composition of this community corresponds well with that described by Bond (1981) as his *Protea lorifolia - Simicheilus multiflorus* community and those described by Campbell (1985) as Cango or Thomas Dry Proteoid Fynbos communities. Some study sites were specifically selected to have areas with different fire histories. The structure of the plant communities differed in these sub-sites, but not the floristic composition. The relative abundance of overstorey proteoid shrubs and/or those of understorey sprouters differed in these sub-sites, which can be ascribed to the fire history of the sites (Kruger 1983; Le Maitre & Midgley 1992).

1.2.2 Study material

The overstorey proteoid shrub species, *Protea eximia*, *P.repens* and *P.lorifolia* are all non-sprouters. In these species, mature plants are killed by fire and they can only re-establish after fire from seed. Seed of these *Protea* species are serotinous and are maintained in cones on the parent plants, until the parents are killed by fire. Once released from the cones the seed is wind-dispersed and may travel through the air for a few meters, after which they will tumble along on the ground until they strike some obstacle. Seed dispersal distance in these species tend to be only a few meters, but it depends on the rockiness of the local terrain (Bond 1988). The species of overstorey proteoid shrubs used in this study exhibit seasonal growth flushes. They are vegetatively inactive during mid-winter, produce new stems during spring-summer (August-March) and flower in autumn-winter (April-July). Points of annual growth flushes remain visible on stems. The number of years which a *Protea* plant grew before it flowered for the first time (juvenile phase) can easily be determined by counting the number of growth flush points on its stem. The juvenile period and longevity of different overstorey proteoid species differ, but the species studied all start flowering when individuals are 0.5 - 0.6 m tall. Within the study area *Protea repens* may need 8-10 years and *P.lorifolia* 10-12 years to reach this height (Vlok 1992). However, depending on site productivity, counterbalanced by competition from sprouters (Figure 1.2), growth rates in these species can vary. The growth pattern and

phenology of overstorey proteoid shrubs have been described in detail by Miller (1985).

In contrast to non-sprouting species, sprouters are species in which some mature plants may survive fires by means of vegetative resprouts from a fire-protected organ (*e.g.* rhizome, lignotuber) after fire (James 1984). Both non- and sprouting plant life forms have been discussed by Keeley *et al* (1981), Gill (1981) and Le Maitre & Midgley (1992). Most of the understorey sprouting species used in this study have a graminoid growth habit and are members of the Restionaceae (*Cannamois scirpoides* and *Hypodiscus striatus*) and Cyperaceae (*Tetraria ustulata*). One species (*Leucadendron salignum*) is a shrub and a member of the Proteaceae. Three species, *Cannamois scirpoides*, *Hypodiscus striatus* and *Leucadendron salignum*, are dioecious. Only female plants were sampled in this study, as sexual fecundity of male plants is more difficult to quantify. The two restioid species differ in size. Mature culms of *C.scirpoides* plants are 1.2 - 1.5 m tall, with those of *H.striatus*, 0.3 - 0,5 m tall. Both these restioid species exhibit clear seasonal growth patterns. They are vegetatively inactive during winter and produce a set of culms at rhizome apices during the spring (August-September). These culms mature and produce seed which are dispersed in the following autumn and early winter (personal observation). The number of culms and seed produced in a season can thus be determined from seasonal growth flushes discernible on excavated rhizomes. The

phenology and growth pattern of *Leucadendron salignum* and *Tetraria ustulata* were described in greater detail by Miller (1985), with his *Restio filiformis* submodel pertaining to *Cannamois scirpoides* and *Hypodiscus striatus*.

1.3 Species diversity indices and semantics

Where I refer to species richness in this dissertation, I simply mean the total number of species in an area of any spatial scale. I generally follow the terminology of Whittaker (1972), with alpha-diversity (α-diversity) and point diversity referring to the **total number of species** within a quadrat. Beta-diversity (ß-diversity) indicates the **turnover rate of species between quadrats**. Beta-diversity is an important factor in this study and I refer to it as the **patchiness of a community**. Others have referred to it as within-community ß-diversity (Whittaker 1972) or as the heterogeneity of a community (Collins & Glenn 1991). The degree to which species have patchy distributions in a community affects the steepness of the slope of a species-area curve (Rosenzweig 1995) and thus, determines the species richness of fynbos and other communities (Bond 1983; Caswell & Cohen 1993).

With overstorey proteas, I indicate non-sprouting shrub species which belong to the Proteaceae family. In the final pyric successional phase of fynbos communities these shrubs tend to form a well developed overstorey canopy over all the

understorey species in a community (Figure 1.1). In the community studied, all overstorey proteoid shrubs were members of the genus *Protea*, but in other mountain fynbos communities members of the genera *Leucadendron* and *Leucospermum* may also be included (Campbell 1985).

CHAPTER 2: THE EFFECT OF OVERSTOREY PROTEAS ON COMMUNITY RICHNESS.

2.1 Introduction

Previous studies in mountain fynbos and related Mediterranean - type shrublands suggested that high densities of overstorey proteas impoverish the species richness of a community. The argument has been that where the species-poor overstorey proteas displace many of the species-rich understorey species, the species richness of a community is reduced (Specht & Specht 1989; Cowling & Gxaba 1990; Esler & Cowling 1990; Keith & Bradstock 1994). However, variances in the temporal and spatial patterning of species in a community should be considered before any conclusion is drawn on the effect which overstorey shrubs have on the persistence of understorey species. In the fynbos the displacement of understorey species may only be temporal, because many species may reappear after a fire in the next fire cycle (Kruger 1983; Kruger & Bigalke 1984). The aim of this chapter is to clarify whether a well-developed canopy of overstorey proteoid shrubs in one fire-cycle affects the α-diversity of understorey species in the following fire-cycle. An important factor that needs to be considered in this study is the spatial scale at which α-diversity is measured. The degree to which species have a clumped or patchy distribution (patchiness component of fynbos communities) can affect the outcome of comparisons of different sites, when α-diversity is measured at different spatial scales (Bond 1983). As yet,

fynbos community patchiness has only been attributed to within-habitat heterogeneity (Cowling *et al* 1992). However, competitive interactions amongst species in fynbos communities may also affect the patchiness of fynbos communities (Yeaton & Bond 1991). Local biotic interaction processes may thus be important in maintaining the patchiness of fynbos communities as they could affect the steepness of the slope of the species-area curve for a community (Rosenzweig 1995). The effect of measuring α-diversity at different spatial scales must thus also be addressed in this study.

To determine how the species richness of a fynbos community is affected by high densities of overstorey proteas, I investigated the following questions in this chapter.

(i) How do high densities of overstorey proteas in one fire-cycle affect the α-diversity levels of a fynbos community in the following fire-cycle, and does the spatial scale at which α-diversity is measured affect these results?

(ii) How do several short fire-cycles and the repeated absence of overstorey proteas affect α-diversity levels in a fynbos community, and are patterns in species richness affected by the spatial scale at which α-diversity is measured?

2.2 Study sites

2.2.1 How does pre-fire density of overstorey proteas affect post-fire α-diversity and does scale of measurement affect the results?

The data to investigate this question were collected at Site One (Chapter 1; Figure 1.2), which covers an area of approximately 500 m X 50 m. The fire history of this site is summarized in Table 2.1.

TABLE 2.1: Fire history of study Site One. (Data determined from unpublished management records of the Swartberg Nature Reserve, Cape Nature Conservation.)

Date of last fire - November 1993
Age of vegetation with last fire - 13 years
Preceding fire frequency - 13 years

The vegetation at this site was 13 years-old when it burned in November 1993. Before the 1993 fire, the overstorey proteas occurred in patches of various sizes and densities. In certain areas the overstorey proteas occurred as dense stands (pre-fire canopy cover percentage 60-80%) while in other intermingled areas they were sparse (pre-fire canopy cover percentage < 30%). Although the 1993 fire was relatively intense, with only thicker (≥ 5 mm) stems and branches of the overstorey proteas remaining after the fire, the pre-burn overstorey density of the proteoid shrubs could still be

determined with reasonable accuracy from the burned skeletons (stems and branches) of the proteoid shrubs.

2.2.2 How does repeated absence of overstorey proteas affect α-diversity and are species-richness patterns affected by scale of measurement?

Data to investigate this question were collected at Site Two (Chapter 1; Figure 1.2) which covers an area of approximately 400m long and 120m wide. Four sub-sites with different fire histories were sampled at Site Two. These fire histories are summarized in Table 2.2.

TABLE 2.2: Layout and fire histories of sub-sites at study Site Two. Double lines indicate 2m wide belts between the sub-sites. Fire dates indicate when sub-sites were burned. Last age indicates the age of the vegetation in each sub-site when the entire study area burned down during 1987. (Data extracted from unpublished management records of the Swartberg Nature Reserve, Cape Nature Conservation.)

400m

SUB-SITE NAME	FIRE BREAK ONE	OLD FYNBOS	FIRE BREAK TWO	MATURE FYNBOS
BURN DATES	1941	1941	1941	1941
	1959	1959	1959	1959
	1965	-	1965	1966
	1971	-	1971	-
	1979	-	1975	-
	1987	1987	1987	1987
AGE TO LAST FIRE	8 years	28 years	12 years	21 years

120m

Site two consists of an area which is dissected by two parallel fire breaks, each approximately 50m wide (hereafter called Fire Break One and Fire Break Two). Both fire breaks were burned repeatedly on a 4 to 6-year rotation during the period 1959 to 1979. Between these two fire breaks a strip of fynbos vegetation, approximately 150m wide, was protected against fire for 28 years (hereafter called Old Fynbos). The vegetation adjacent to the second fire break was burnt on an intermediate fire-cycle, with one short 7-year cycle and thereafter protected against fire for 21 years (hereafter called Mature Fynbos). During March 1987 the entire study site (both fire breaks, Mature and Old Fynbos) burned due to a lightning-caused fire. This fire was also relatively hot and did not leave unburnt leaves on overstorey shrubs or unburnt patches of vegetation within the area. If any, few overstorey proteas occurred in the two fire breaks over the last three fire-cycles (determined from aerial photographs). In the less frequently burned Mature and Old Fynbos sites the overstorey proteas persisted throughout the period for which the fire breaks were regularly burned. Before the 1987 fire, the canopy cover percentage of overstorey proteas in the Mature Fynbos varied in intermingled patches from 0% to 75%, while those in the Old Fynbos area varied between 45% to 90% (determined from burned skeletons of overstorey proteas). The presence of a few overstorey proteas in the two fire breaks, when data were collected in 1995, can be explained from wind dispersal of seed

from the adjacent Mature and Old Fynbos sites when the entire area burned in 1987.

2.3 Methods

2.3.1 How does pre-fire density of overstorey proteas affect post-fire α-diversity and does scale of measurement affect the results?

The data to investigate how high densities of overstorey proteas in one fire-cycle affect the α-diversity of a fynbos community in the following fire-cycle were collected from Site One. These data were collected during March and May 1995 when the newly regenerating fynbos vegetation was approximately 1.5-years-old, after the 1993 fire. The post-fire α-diversity values of understorey species, in relation to pre-fire overstorey percentage, were determined from quadrats situated where the canopy cover of the overstorey proteas differed before the last fire. The canopy cover percentage, which the overstorey proteas had before the 1993 fire, was measured from the skeletons (stems and branches) of the burned proteoid shrubs. The burned protea skeletons remained standing and were still largely intact when data were collected in 1995. The canopy cover percentage of overstorey proteas was calculated as the percentage of a quadrat covered by branches and stems of overstorey proteas before the fire. Thus, for each quadrat; (i) the pre-fire canopy cover percentage of overstorey proteas was determined, (ii) the number of overstorey proteas which

occurred within the quadrat was counted and, (iii) the total number of angiosperm species which regenerated after the fire in a quadrat was determined. These data were collected for thirty quadrats each of four sizes; 1X1m (1-m^2), 2X2m (4-m^2), 5X5m (25-m^2) and 10X10m (100-m^2). To ease data collection, the first twenty quadrats were nested, but an additional ten quadrats were sampled for each size class to ensure that the full range of canopy densities, which the overstorey proteas had at the site, were obtained. For each quadrat size, the thirty replicates did not overlap in surface area. To ensure that surface rock cover was approximately equal in each quadrat, the quadrats were situated at positions where the percentage surface rock cover ranged from 5-10% of a quadrat's surface area.

Werger (1972) suggested that quadrats in fynbos vegetation should be large enough to contain an average of 50-55% of the species within the sampled community if the species richness of a community is to be measured. To determine which quadrat size would give a reasonable estimate of the species richness of the fynbos community, the entire study site area was traversed and the total number of angiosperm species which occurred on the site was determined. The mean number of species encountered in the 1-m^2, 4-m^2, 25-m^2 and 100-m^2 quadrats were calculated to determine which quadrat sizes would contain $\geq$ 50% of the total number of species encountered at Site One.

For each quadrat size, the total number of understorey species in a quadrat was correlated against the canopy cover percentage which the overstorey proteas had before the 1993 fire (hereafter called pre-fire canopy percentage). Similarly, the total number of understorey species in a quadrat was correlated against the number of overstorey protea shrubs which occurred in a quadrat (hereafter called pre-fire shrub density). After the relationship between pre-fire canopy percentage and total number of understorey species was determined, the understorey species were classed into different guilds. The relationship between pre-fire canopy percentage and number of species of a specific guild were then determined for the 100-m^2 quadrats. The guilds of understorey species were; (i) non-sprouting understorey species, (ii) sprouting understorey species, (iii) ephemeral and herb species (all species which are short-lived, with a maximum post-fire life span of 5 years), (iv) non-ephemeral species (all species with a post-fire life span exceeding 5 years). For each data set from the 1-m^2, 4-m^2, 25-m^2 and 100-m^2 quadrats, Spearman Rank Correlation Coefficients were used to determine if a relationship exists between pre-fire overstorey canopy percentage and the total number of understorey species in the quadrats (Siegel & Castellan 1988). A similar protocol was followed to determine if a significant relationship exists between pre-fire overstorey shrub density and the number of species of a specific guild for the 100-m^2 quadrats.

2.3.2 How do repeated absence of overstorey proteas affect α-diversity and are species-richness patterns affected by scale of measurement?

Data to investigate this question were collected at Site Two, during April 1995, when the fynbos vegetation was 8-years-old. The α-diversity values of understorey species (number of species per quadrat) in the four sub-sites (two fire breaks, Mature and Old Fynbos) were compared. The α-diversity values were determined by enumerating all the angiosperm understorey species in twenty 100-m^2, randomly located quadrats, in each of the two fire breaks, the Mature Fynbos and the Old Fynbos sub-sites. The quadrats were restricted to an area of 115 X 40m in each of the sub-sites. The areas within these sub-sites were identical in elevation, slope angle and aspect. A Spearman Rank Correlation Coefficient was calculated for the relationship between number of understorey species in 100-m^2 quadrats and number of times a sub-site was burned during the past 28 years (Siegel & Castellan 1988). A Kruskal-Wallis Analysis of Variance Test was used to compare the α-diversity values of understorey species in the two fire breaks, Mature Fynbos and Old Fynbos sub-sites (Siegel & Castellan 1988).

I also compared understorey species α-diversity values from Fire Break One with those of the Old Fynbos sub-site, to determine if α-diversity values from a site where the overstorey proteas have been repeatedly absent for several

fire-cycles differ from those of a site where the overstorey proteas persisted. Twenty 1-m^2, 4-m^2 and 100-m^2 randomly located quadrats were sampled for each of these two sub-sites to determine if different sized quadrats give different results. The total number of angiosperm understorey species which occurred in the total area of each sub-site, was also determined. The data from each set of these differently sized quadrats, in the Fire Break One and Old Fynbos sub-sites, were compared by means of Wicoxon-Mann-Whitney tests (Siegel & Castellan 1988).

A Spearman Rank Correlation Coefficient was calculated for the relationship between pre-fire overstorey percentage and post-fire α-diversity of understorey species, for a combined data base of all the data collected from the four sub-sites sampled at study Site Two, with twenty 100-m^2 quadrats sampled in each of the two fire breaks, Mature and Old Fynbos sub-sites (Siegel & Castellan 1988). Following the same protocol, a similar correlation coefficient was also calculated for the quadrats sampled in the Mature Fynbos sub-site. This correlation coefficient could not be calculated for the other three sub-sites because a limited range of pre-fire overstorey densities occurred in the two fire breaks and the Old Fynbos sites. The vegetation in these sub-sites was 8-years-old when the pre-fire canopy percentage of overstorey proteas was measured and the burned skeletons of the overstorey proteas were no longer completely intact. The pre-fire canopy

percentage of the overstorey proteas could thus not be measured with accuracy at Site two and given values may be somewhat lower than what they actually may have been.

2.4 Results

2.4.1 How does pre-fire density of overstorey proteas affect post-fire α-diversity and does scale of measurement affect the results?

A total of 87 species were encountered at study Site One. Community species richness was only sampled adequately in 100-m^2 quadrats at Site One. The number of species in quadrats only met the prerequisite of 50-55% of the total number of species in the study area in the 100-m^2 quadrats (Table 2.1).

TABLE 2.1: Means of number of species (standard errors) and percentages sampled of the total number of species at the site in differently sized quadrats at study Site One.

QUADRAT SIZE	NUMBER OF SPECIES	PERCENTAGE OF TOTAL
1-m^2	19.4 (0.62)	22.3%
4-m^2	29.4 (0.77)	33.8%
25-m^2	40.9 (0.91)	47.0%
100-m^2	48.9 (1.01)	56.2%

No significant correlations were found between pre-fire canopy percentage of the overstorey proteas and post-fire

number of understorey species for the 1-m² and 4-m² quadrats. However, significant positive correlations were found between pre-fire canopy percentage of the overstorey proteas and the post-fire number of understorey species for 25-m² ($P < 0.01$) and 100-m² ($P < 0.005$) quadrats (Figure 2.1). In addition, a significant correlation was also found between number of pre-fire overstorey plants and number of understorey species for the 100-m² quadrats ($P < 0.005$). The highest number of understorey species were only found where more than 30 overstorey protea plants occurred in a 100-m² quadrat.

For specific species guilds the relationship between pre-fire canopy percentage of the overstorey proteas and number of species in 100-m² quadrats followed a similar pattern to those for the total number of understorey species in quadrats. A positive correlation was found between the number of sprouting understorey species and pre-fire canopy percentage of the overstorey proteas ($P < 0.02$). Significant correlations were also found between pre-fire canopy percentage of the overstorey proteas and number of post-fire understorey species for ephemeral and herb species ($P < 0.04$) and non-ephemeral understorey species ($P < 0.01$). The highest number of ephemeral and herb species and non-ephemeral species, occurred where the canopy percentage of the overstorey proteas was high (>50%) before the last fire. The only guild in which no significant relationship was found between pre-fire canopy percentage of the overstorey proteas and post-fire number of understorey

species, was the non-sprouting understorey species ($P < 0.06$; Table 2.2).

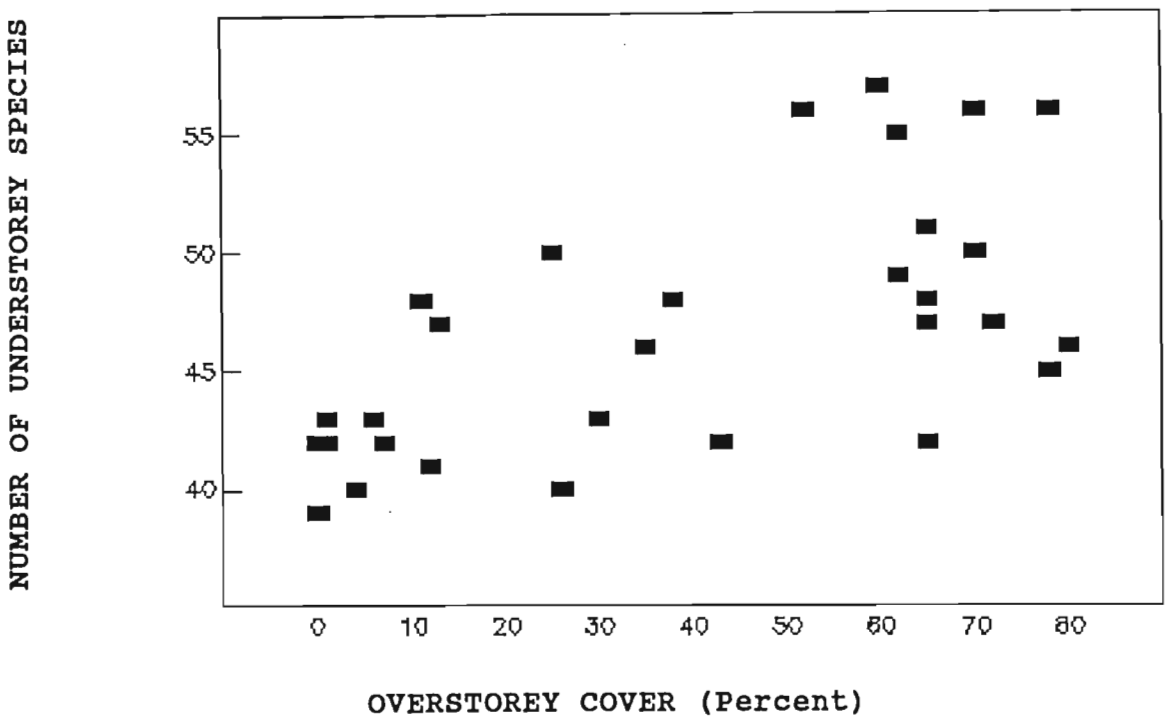

FIGURE 2.1: Total number of understorey species in one-year-old mountain fynbos in relation to the canopy cover percentage of overstorey proteas in the previous fire. Data from thirty 100-m² quadrats.

TABLE 2.2: Correlation between number of understorey species in a guilds of species and percentage canopy percentage of overstorey proteas before the last fire. (Significant positive correlation indicated with an asterisk; quadrat size = 100-m² and n = 30)

SPECIES GUILD	R_S VALUE	SIGNIFICANCE
SPROUTING SPECIES	0.44	$P < 0.02^*$
NON-SPROUTING SPECIES	0.36	$P < 0.06$
EPHEMERAL & HERB SPECIES	0.40	$P < 0.04^*$
NON-EPHEMERAL SPECIES	0.58	$P < 0.01^*$

2.4.2 How do repeated absence of overstorey proteas affect α-diversity and are species-richness patterns affected by scale of measurement?

The data from 100-m² quadrats also met the prerequisite of 50-55% of the species in a community at the sub-sites of Site Two (Table 2.3). The mean α-diversity of understorey species in the 100-m² quadrats and the total number of species found at a sub-site decreased with an increase in the number of times a sub-site has burned during the past 28 years (Table 2.3). A significant correlation was found between the number of species in 100-m² quadrats and the number of times the sub-sites burned in the past 28 years ($P < 0.001$). More frequently burned sub-sites had less species in 100-m² quadrats than sub-sites burned infrequently. A significant difference was found in the number of species in 100-m² quadrats when the data from the two fire breaks, the Mature Fynbos and Old Fynbos sub-sites were

compared ($P < 0.001$). However, when data from the Old Fynbos sub-site were excluded from the database, to determine if data of the Old Fynbos sub-site caused the significant difference, no significant difference was found between the α-diversity values in the two fire breaks and that of the Mature Fynbos sub-site (Table 2.3).

TABLE 2.3: Mean number of species in 100-m² quadrats and total number of species encountered at the sub-sites of study Site Two. Percentage of species sampled in a 100-m² quadrat from total number of species encountered at a this sub-site and number of times each sub-site was burned during the previous are indicated. Standard error for number of species are in parentheses, with n = 20. Different superscripts indicate statistical difference at $P < 0.01$ level.

SUB-SITE	NUMBER OF SPECIES MEAN	TOTAL	PERCENTAGE	NUMBER OF BURNS
FIRE BREAK ONE	39.9 (0.83)[a]	72	55.4%	4
FIRE BREAK TWO	40.1 (0.56)[a]	72	55.7%	4
MATURE FYNBOS	41.2 (0.98)[a]	75	54.9%	2
OLD FYNBOS	45.5 (0.82)[b]	94	48.4%	1

In a combined data base, for all four sub-sites of study Site Two, a significant positive correlation was found between canopy percentage of the overstorey proteas before the last fire and number of understorey species in 100-m² quadrats after the fire ($P < 0.001$; Figure 2.2). A similar significant correlation was also found for the Mature Fynbos sub-site ($P < 0.001$). This correlation could not be done for the other three sub-sites because the canopy cover percentages of the

overstorey proteas were either only low (< 1% in two fire breaks) or only high (45-95% in Old Fynbos) within the sub-sites (Figure 2.2).

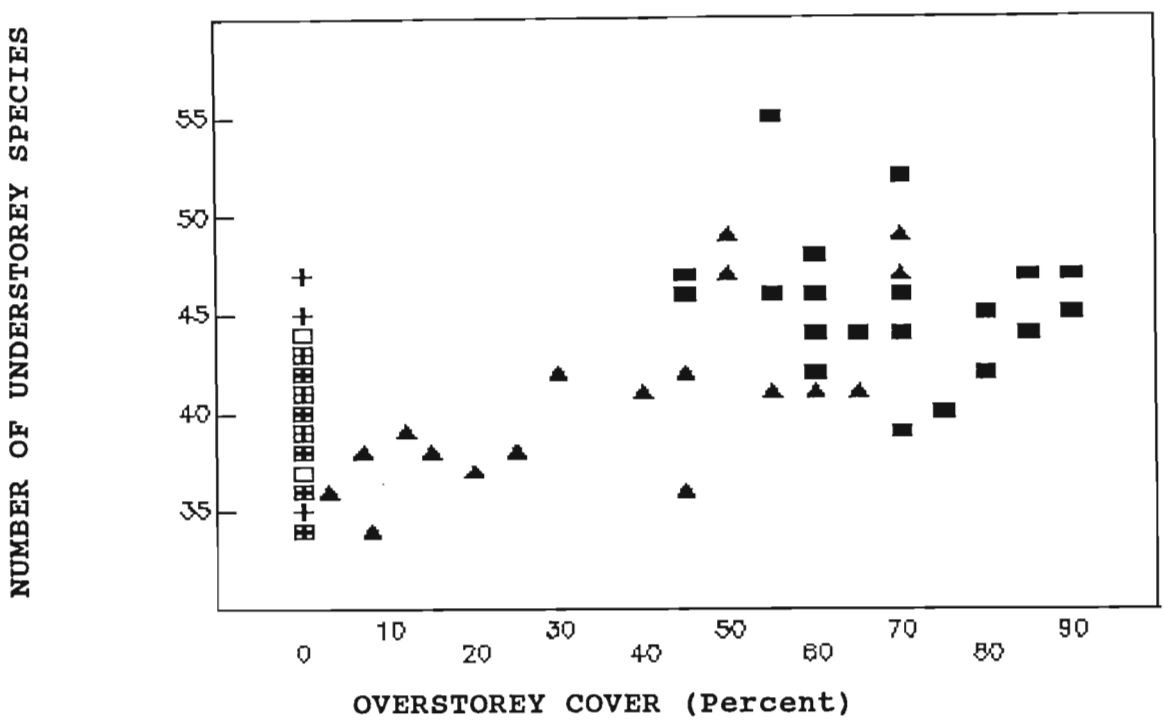

FIGURE 2.2: Number of understorey species in 100-m² quadrats in relation to the canopy percentage of overstorey proteas before the last fire. Twenty randomly located quadrats were sampled in each of four adjacent sub-sites. Open squares and plus signs show data from sites where overstorey proteas were absent before the last burn (Fire Break One & Two). Solid triangles indicate data from site where overstorey proteas were present and 21 years old before the last burn (Mature Fynbos) and solid squares indicate data from site where overstorey proteas were present and 28 years old before the last burn (Old Fynbos).

Similarly to the result noted in section 2.4.1, results of comparing α-diversity of understorey species in Fire Break One with those of the Old Fynbos sub-site depended on the spatial scale at which α-diversity was measured. In small quadrats (1-m^2 and 4-m^2) the mean number of species recorded in quadrats was significantly higher in Fire Break One than those recorded in the Old Fynbos ($P < 0.05$). This was not the case where α-diversity values were compared for 100-m^2 quadrats. In the 100-m^2 quadrats the α-diversity was significantly higher in the Old Fynbos sub-site than in the Fire Break One sub-site ($P < 0.001$; Table 2.4).

TABLE 2.4: Mean number of species (with standard errors) for differently sized quadrats in two adjacent 8-year-old mountain fynbos sites burned at different fire-cycles. The Fire Break was burnt 4 times at a 6-year fire cycle and lacked overstorey proteas during the last two fire-cycles, whilst the Old Fynbos was protected from fire for 28 years and had a well-developed canopy of overstorey proteas before the last fire. Data from 20 randomly located quadrats for each of the quadrat sizes.

	FIRE BREAK	OLD FYNBOS
1X1m	14.95 (0.605)	11.80 (0.635)
2X2m	22.00 (0.673)	19.90 (0.965)
10X10m	39.85 (0.825)	45.45 (0.816)

2.5 Discussion

Results from both study Site One, which was 13-years old when burned, and Site Two, with a complex fire history, indicate that overstorey proteas play an important role in maintaining the species richness of fynbos communities. In 100-m² quadrats, the highest number of understorey species were only found where the pre-fire canopy percentage of overstorey proteas was high (> 50%) and where the overstorey protea shrubs occurred at high densities (≥ 30 plants per 100-m²). The post-fire species richnesses of several guilds of understorey species were enriched by high pre-fire canopy densities of overstorey proteas. The survival of many understorey species, particularly herbs and ephemeral species may depend on the presence of a well-developed canopy of overstorey proteas in a community. Where overstorey proteas persisted, the total number of understorey species was approximately 22% more than in similar sized sites where the overstorey proteas have been lacking for several fire-cycles. These results contradict those from previous studies in fynbos vegetation (Cowling & Gxaba 1990; Esler & Cowling 1990) and other related Mediterranean-type shrublands (Keith & Bradstock 1994). The importance of considering results from different spatial scales of measurement was not comprehended by previous workers. They only studied the effect of high overstorey density on the species richness of understorey species at a small spatial scale, in quadrats of 1-4-m² (Cowling & Gxaba 1990; Esler & Cowling 1990;

Keith & Bradstock 1994). Results from this study demonstrate how important it is to consider results from different spatial scales of measuring α-diversity before conclusions are drawn for community-wide species richness. At study Site One, no relationship could be found between pre-fire canopy percentage of overstorey proteas and the post-fire α-diversity levels of understorey species for quadrats of < 5-m^2, but a significant relationship was found when data from quadrats of ≥ 25-m^2 were used. Similarly, at study Site Two, small quadrats (< 5-m^2) gave different results to larger (100-m^2) quadrats. Here the α-diversity of understorey species was higher where overstorey proteas were lacking than where they were dense when data from small quadrats (< 5-m^2) were compared. The opposite relationship was found when data from larger (100-m^2) quadrats were compared. This disparity in results can be attributed to the patchiness component of fynbos communities (Bond 1983). The effect which a clumped distribution of species has on the species richness of an area cannot be measured in small quadrats (< 5-m^2), but in larger quadrats it will be incorporated in the results. Results from both study areas indicate that overstorey proteas not only affect α-diversity levels of understorey species, but also affect the within-community ß-diversity or the patchiness of species in a community. Although the overstorey proteas displace species at a small spatial scale (< 5-m^2), a patchy displacement of species will result in an increase in the within-community ß-diversity, which will result in an overall increase in the

species richness of understorey species at larger spatial scales. Biotic interactions occurring amongst species, such as competitive interactions, will not only affect the intercept (α-diversity) of a species-area curve but also the steepness of the slope (ß-diversity).

Differences in the species-richness patterns between the sub-sites of study Site Two may be due only to differences in the fire histories of the sub-sites, rather than to the previous history relating to coverage of the overstorey proteas. However, the positive relationship between post-fire understorey α-diversity and pre-fire presence of overstorey proteas found at both study sites, despite differences in their fire history, suggest that fire regime and the presence of overstorey proteas have an important effect on the persistence of understorey species. Decoupling cause and effect of a fire regime on species diversity patterns is notoriously difficult, for the fynbos and other vegetation types (Collins *et al* 1995). For the fynbos it would be a futile exercise to attempt to uncouple fire regime effects on species diversity patterns from those of the overstorey proteas. These two factors are not independent because the regeneration success of overstorey proteas depends on the local fire regime (Kruger 1983; Le Maitre & Midgley 1992). For example, the phytomass of overstorey proteas affect the fire intensity of a fire regime (Van Wilgen & Richardson 1985; Bond & Van Wilgen 1996).

Although it is clear that overstorey proteas should be maintained if the species richness of fynbos communities is to be conserved, I am unable to conclude at what densities these overstorey shrubs should be conserved. The data from the first study site suggest that the relationship between the percentage of overstorey proteas and α-diversity of understorey species is sigmoid. The highest number of understorey species occurred at a density of approximately 50 overstorey proteas per 100-m^2. However, it seems unlikely that some optimum density of overstorey proteas would result in maximum community species richness as overstorey proteas tend to be clumped in southern Cape fynbos communities (Bond 1988; Midgley & Watson 1992). The clumped distribution of overstorey proteas and the positive relationship between canopy percentage and certain guilds of understorey species, supports the notion that overstorey proteas may be important in maintaining the patchiness of fynbos communities. At both study sites the overstorey canopy was not completely closed, even in relatively dense stands of overstorey proteas. At a spatial scale of 100-m^2, gaps were present in the overstorey canopy cover. A clumped distribution of overstorey proteas, rather than a continuous dense canopy cover, seems to be important for maintaining the patchiness of understorey species in fynbos communities. In this aspect I agree with the conclusions of Cowling & Gxaba (1990) that the persistent presence of high densities of overstorey proteoid shrubs may displace certain understorey species. More

importantly, the persistent lack of proteoid shrubs will also result in the local extinction of certain understorey species.

In many vegetation types of the world, plant community and landscape diversity values are inter-dependent and determined by local and regional processes. The regional species pool may affect species immigration rates into communities while local competitive interactions amongst species may affect α-diversity values (Ricklefs 1987; Collins & Glenn 1991; Ricklefs & Schluter 1993). In fynbos vegetation, most under- and overstorey species have short seed dispersal distances and many are habitat specialists (Campbell & van der Meulen 1980; Bond & Slingsby 1983; Manders 1986; Bond 1988). Thus it is unlikely that the regional species pool will enhance species immigration into fynbos communities greatly. Results from this study indicate that the species richness of mountain fynbos communities is maintained by dynamics processes which determine the patchiness of understorey species in a community. This effect is largely induced by the variability in the canopy cover percentage of the local overstorey proteas rather than by frequent long-distance immigration events of species from neighboring sites.

2.6 Conclusions

1. High pre-fire canopy cover percentages and densities of overstorey proteas have a positive effect on the post-fire α-diversity levels of understorey species. The α-diversity of several guilds of understorey species were enhanced by high pre-fire canopy percentages of overstorey proteas.

2. In sites where one or more short fire-cycles resulted in the repeated absence of overstorey proteas, α-diversity levels of understorey species were lower than at a site where overstorey proteas persisted.

3. These conclusions are dependant on the spatial scale at which α-diversity of understorey species are measured. When α-diversity values are measured in quadrats of < 5 -m^2, different conclusions will be drawn to those where quadrats of 100-m^2 are used. The contradiction in conclusions when α-diversity is measured at different spatial scales can be attributed to the patchiness component of fynbos communities. Where small quadrats (< 5 -m^2) are used, the patchiness component (within-community turnover rate of species) is not included, but where larger quadrats (100-m^2) are used, the patchiness component is included.

4. The results of this chapter indicate that overstorey proteas play an important role in maintaining the patchiness component of fynbos communities. Local dynamic interactions between overstorey and understorey species are important in generating and maintaining the species richness of fynbos communities.

CHAPTER 3: THE EFFECT OF SEVERAL SHORT FIRE-CYCLES ON THE BASAL COVER PERCENTAGE AND DENSITY OF UNDERSTOREY SPROUTING SPECIES.

3.1 Introduction

In Mediterranean-type shrublands, the prevalent fire regime can affect the proportion of sprouting to non-sprouting species in a community. Short fire-cycles of 3-10 years generally favour sprouting species, whilst longer periods between fires (> 10 years) tend to favour non-sprouting species (Keeley & Zedler 1978; Kruger 1983; Bell *et al* 1987; Keith & Bradstock 1994; van Wilgen *et al* 1994). Keeley & Zedler (1978) explained this observation by a model for Californian chaparral where regeneration success of non-sprouting species depends on the number of regeneration "gaps" available after a fire. More regeneration "gaps" are available after long inter-fire periods, as an increasing number of non-sprouters and sprouters become senescent. Also, due to higher fuel volumes accumulating over long periods of time, fire intensities are higher and even more sprouters may be killed.

The general pattern, of sprouters being more abundant in frequently burned sites than in areas which have long inter-fire periods, has been accepted for most Mediterranean-type shrublands (Kruger 1983). The processes, which maintain these patterns in the different communities may, however, differ from

those proposed by Keeley & Zedler (1978). The relative density of sprouters may depend not only on the fire frequency, but also on soil moisture availability in an area. Non-sprouters may be rare or absent in well-watered areas because sprouters are able to re-establish so rapidly after a fire in wet areas, that they fill most of the regeneration "gaps" which would have been available to non-sprouter species (Specht 1981; Bell *et al* 1987; Le Maitre & Midgley 1992). This prediction is, however, not consistent for all observations in the fynbos. Tall non-sprouting overstorey species may also be common in well-watered fynbos habitats (Kruger 1983; Schutte *et al* 1995).

The competitive interactions amongst non-sprouting overstorey and sprouting understorey species may also affect the relative abundance of sprouters. If overstorey proteas are able to inhibit the growth of sprouters, then sprouters will become abundant where short frequency fire regimes have eliminated the overstorey proteas. This study was conducted to investigate if the basal cover and/or density of sprouting understorey species increase in a fynbos community where overstorey proteas have been repeatedly absent due to several short fire-cycles.

3.2 Study site

Data were collected at three sub-sites of study Site Two, which is described in more detail in Chapter 1. The layout of the

three sub-sites sampled at study Site Two and their fire histories are summarized in Table 3.1.

TABLE 3.1: Layout and fire history of three sub-sites sampled at study Site Two. Double lines indicate 2m wide belts between the sub-sites. Burn dates indicate years in which the sub-sites were burned. Vegetation age indicates the age of the vegetation in each sub-site when the entire study area burned down during 1987.

250m

SUB-SITE	FIRE BREAK ONE	OLD FYNBOS	FIRE BREAK TWO	
BURN DATES	1941	1941	1941	
	1959	1959	1959	
	1965	-	1965	120m
	1971	-	1971	
	1979	-	1975	
	1987	1987	1987	
VEGETATION AGE	8 years	28 years	12 years	

Site Two consists of an area which is dissected by two parallel fire breaks, each approximately 50m wide (hereafter called Fire Break 1 and Fire Break 2). Both fire breaks were burned on a 4- to 6-year rotation during the period 1959 to 1979. Between these two fire breaks a strip of fynbos vegetation, approximately 150m wide, was protected against fire for 28 years (hereafter called Old Fynbos). During March 1987 the entire study site (both fire breaks and the Old Fynbos) burned down. The vegetation of the Old Fynbos sub-site differed only from those of the two fire breaks in the relative

abundance of the overstorey proteoid shrubs. The mean pre-fire cover percentage of the overstorey proteas was 68.5% (S.E. 3.1%) in the Old Fynbos and < 1% in the two fire breaks. Fire Break 1 lacked overstorey proteas for at least two fire-cycles, while these shrubs were lacking from Fire Break 2 for at least one fire-cycle (determined from aerial photographs). The lack of non-sprouting overstorey proteoid shrubs in these two fire breaks can be attributed to the repeated short-cycle fires at which the two fire breaks were burned. *Protea eximia*, *P.repens* and *P.lorifolia* were the dominant overstorey proteoid shrubs and *Brunia nodiflora*, *Cyclopia intermedia* and *Leucadendron salignum* the dominant sprouting understorey shrubs in the Old Fynbos. *Cannamois scirpoides*, *Hypodiscus striatus* and *Tetraria ustulata* were the dominant sprouting understorey graminoids in both fire breaks and the Old Fynbos (Appendix 1).

3.3 Methods

Data were collected during June 1995, when the vegetation of both fire breaks and Old Fynbos was 8 years old. Densities and basal cover of sprouting species in the two fire breaks were determined by means of the ellipse-intercept method (Stokes & Yeaton 1994). This technique requires that a transect line is laid through the study site and that the longest axis (length) of each plant intercepted by the transect line and greatest width at right angles to its length are measured and used to calculate its basal area. To calculate cover and density values

of the sampled area, the sum of the contribution of each plant intercepted by the transect line is determined. Percentage cover and plant density values were then determined (Stokes & Yeaton 1994). In my study, cover and density values of sprouting species in the three sub-sites (Fire Break 1 & 2 and Old Fynbos) were determined by laying out ten 20-m long transects, each 3m apart and parallel to one another, in each sub-site. Only the long and short axes of the basal area of sprouter species plants were recorded. Where plants of more than one sprouter species were intermingled, to form solid clumps of several sprouter species (which was often the case with graminoid species which formed heterogeneous species clumps in a single tussock), the long and short basal axes of the entire clump of sprouting species were measured to determine cover values. The number of sprouting plants in each of three size classes, those which contributed < 0.5%, 0.5-1.0% or > 1.0% to the basal cover percentage of a transect, were also determined for all the transects in the three sub-sites.

The Stokes & Yeaton (1994) technique was also used to determine the basal cover percentages and densities of certain individual sprouter species which could be clearly defined as individual plants in the three sub-sites. These data were obtained by recording the long and short basal axes of all *Cannamois scirpoides*, *Hypodiscus striatus*, *Leucadendron salignum* and *Tetraria ustulata* plants intercepted along ten 50m

transects, also parallel to each other and 3m apart, in each of the two fire breaks and Old Fynbos sub-sites.

Kruskal-Wallis analysis of variance tests were used to determine if sprouting species cover and/or density values differed significantly between the three sub-sites. Where significant ($P < 0.05$) Kruskal-Wallis values were found, multiple comparisons between sub-site cover and density values were conducted to determine which sub-sites differed significantly in their basal cover or density of the sprouting species. A similar protocol was followed to analyze data for the dominant sprouter species studied (Siegel & Castellan 1988).

3.4 Results

In the two fire breaks the mean basal cover percentage of sprouting species was approximately 32% more than those of the Old Fynbos site ($P < 0.001$; Table 3.2). The mean density of sprouter plants was significantly higher in Fire Break 1 than in Fire Break 2 ($P < 0.05$), but the density of sprouters in the Old Fynbos did not differ significantly from those in the two fire breaks (Table 3.2). Although the mean density of sprouter plants in the Old Fynbos did not differ from those in the two fire breaks, there were significantly less large sprouter plants in the Old Fynbos than in the two fire breaks ($P < 0.01$;

Table 3.3). Fire Break 1 also had significantly more small sprouter plants than Fire Break 2 ($P < 0.05$).

TABLE 3.2: Mean and standard errors for basal cover percentages and densities of sprouting species on ten 20-m transects in 8-year-old mountain fynbos sites with different fire histories. (Same superscripts down a column indicate no statistical differences with $P > 0.05$.)

	BASAL COVER (%)	DENSITY (# plants/m²)
FIRE BREAK 1	32.2 (1.40)^{a}	5.9 (0.44)^{a}
FIRE BREAK 2	31.7 (0.66)^{a}	3.8 (0.48)^{b}
OLD FYNBOS	24.1 (0.74)^{b}	5.8 (0.84)^{ab}

TABLE 3.3: Mean number of sprouter plants in three size classes on ten 20-m transects in 8-year-old mountain fynbos sites with different fire histories. Plants were classed in a size class on the percentage cover each plant contributed to the basal cover percentage of a transect. (Standard errors in parentheses; same superscripts down a column indicate no statistical differences with $P > 0.05$.)

	SMALL (< 0.5%)	MEDIUM (0.5-1%)	LARGE (> 1.0%)
FIRE BREAK 1	5.2 (0.85)^{a}	8.5 (1.12)^{a}	14.2 (1.03)^{a}
FIRE BREAK 2	1.9 (0.84)^{b}	5.7 (1.00)^{a}	15.0 (0.67)^{a}
OLD FYNBOS	4.8 (1.09)^{ab}	8.6 (1.28)^{a}	10.0 (0.75)^{b}

The individual sprouter species varied in their responses to the different fire histories of the sub-sites. The basal cover percentages of all the investigated species (*Leucadendron salignum*, *Cannamois scirpoides*, *Hypodiscus striatus* and *Tetraria ustulata*) did not differ significantly between Fire

Break 1 and Fire Break 2, or between Fire Break 2 and the Old Fynbos sub-sites. The basal cover percentages were significantly lower at the Old Fynbos than in Fire Break 1 for *Leucadendron salignum* ($P < 0.001$; Table 3.4), *Cannamois scirpoides* ($P < 0.001$; Table 3.5) and *Hypodiscus striatus* ($P < 0.05$; Table 3.6). Plant densities were also significantly lower at the Old Fynbos than in Fire Break 1 for *Leucadendron salignum* ($P < 0.001$; Table 3.4) and *Cannamois scirpoides* ($P < 0.001$; Table 3.5), but not in *Hypodiscus striatus* (Table 3.6). Results of *Tetraria ustulata* differed from the general pattern of the other sprouter species. The basal cover percentages of this species did not differ significantly between the three sub-sites, but plant density was significantly lower in Fire Break 2 than at the other two sub-sites ($P < 0.01$; Table 3.7).

TABLE 3.4: Mean and standard errors for basal cover percentages and densities of *Leucadendron salignum* on ten 20-m transects in 8-year-old mountain fynbos sites with different fire histories. (Same superscripts down a column indicate no statistical differences with $P > 0.05$.)

	BASAL COVER (%)	DENSITY (# plants/m²)
FIRE BREAK 1	3.2 (0.53)^{a}	0.6 (0.10)^{a}
FIRE BREAK 2	4.6 (0.61)^{ab}	0.9 (0.12)^{a}
OLD FYNBOS	1.2 (0.29)^{b}	0.2 (0.04)^{b}

TABLE 3.5: Mean and standard errors for basal cover percentages and densities of *Cannamois scirpoides* on ten 20-m transects in 8-year-old mountain fynbos sites with different fire histories. (Same superscripts down a column indicate no statistical differences with $P > 0.05$.)

	BASAL COVER (%)	DENSITY (# plants/m²)
FIRE BREAK 1	5.3 (0.74)^{a}	1.1 (0.17)^{a}
FIRE BREAK 2	2.8 (0.51)^{ab}	0.9 (0.23)^{ab}
OLD FYNBOS	0.9 (0.24)^{b}	0.4 (0.09)^{b}

TABLE 3.6: Mean and standard errors for basal cover percentages and densities of *Hypodiscus striatus* on ten 20-m transects in 8-year-old mountain fynbos sites with different fire histories. (Same superscripts down a column indicate no statistical differences with $P > 0.05$.)

	BASAL COVER (%)	DENSITY (# plants/m²)
FIRE BREAK 1	5.0 (0.32)^{a}	3.1 (0.31)^{a}
FIRE BREAK 2	4.4 (0.42)^{ab}	2.6 (0.26)^{a}
OLD FYNBOS	3.2 (0.40)^{b}	2.4 (0.23)^{a}

TABLE 3.7: Mean and standard errors for basal cover percentages and densities of *Tetraria ustulata* on ten 20-m transects in 8-year-old mountain fynbos sites with different fire histories. (Same superscripts down a column indicate no statistical differences with $P > 0.05$.)

	BASAL COVER (%)	DENSITY (# plants/m²)
FIRE BREAK 1	7.0 (0.52)^{a}	1.5 (0.15)^{a}
FIRE BREAK 2	5.7 (0.58)^{a}	0.7 (0.10)^{b}
OLD FYNBOS	7.0 (0.62)^{a}	1.5 (0.20)^{a}

3.5 Discussion

The results of this study support previous observations that the basal cover percentage of sprouting understorey species is higher in sites which were subjected to several short fire-cycles than at sites burned at longer fire-cycles (Kruger 1983; Keith & Bradstock 1994). The density of sprouter plants may not be affected by the fire history of a site, but more large plants of sprouter species occur at sites burned at short fire-cycles than at sites burned at longer fire-cycles. Sprouters may be partially favoured by several short fire-cycles due to the fact that overstorey proteas are absent from such sites. However, it is not possible to ascribe the increase in basal area and/or density of understorey sprouters only to the lack of overstorey proteas as sprouting species may also respond to other factors associated with short fire-cycles. For instance, fire intensity may also be linked to a lack of overstorey species. The relatively large biomass of overstorey species may add considerably to the fuel load of a fire. Increased fuel loads add to the intensity of a fire, killing sprouters (Keeley & Zedler 1978, Van Wilgen & Richardson 1985). Results from this study suggest that the reasons why sprouters are favoured by short-cycle fire regimes in the fynbos are as follows; (i) where overstorey proteas are absent, the basal cover of established sprouter plants gradually increase until several adjacent sprouter plants (tussocks) merge to form large clumps of sprouters; (ii) if more fires occur in the absence of

overstorey proteas, the basal cover percentage of sprouters remains high, but the densities of sprouters increase.

Individual sprouting species may vary in their response to fire regimes (Le Maitre *et al* 1992). The results of this study indicate that the basal cover percentage and density of sprouting species, such as *Leucadendron salignum* and *Cannamois scirpoides*, may increase after several short fire-cycles. Other species, such as *Tetraria ustulata*, may only respond in their numbers and not in basal cover to short fire-cycles. The general improved performance of understorey sprouters under a short-cycle fire regime may be due to release of competition from overstorey proteas, as several short-cycle fires will kill the overstorey proteas (Kruger 1983). Variability in response to short-fire cycles of the different sprouter species may thus be due to variability in the sensitivity of some understorey sprouters to competition from overstorey proteas. If this is so, then I would predict that a species such as *Hypodiscus striatus* (which did not respond in its density to the different fire regimes in this study) would be less vulnerable to competition from overstorey proteas than *e.g. Cannamois scirpoides* and *Leucadendron salignum* (which did respond in their density and basal cover percentages to the different fire regimes in this study). This aspect and prediction will be dealt with in Chapter 5.

3.6 Conclusions

1. The density of sprouting species may not be affected by the prevalent fire regime. However, individuals of sprouting species (or clumps of several sprouter species) are larger (with higher basal cover percentages) at sites burned at short fire-cycle regimes than at sites burned at long fire-cycles. The higher number of large sprouters at frequently burned sites result in an increase in the mean basal cover percentage of sprouters at such sites.

2. Different understorey sprouting species vary in their response to short-cycle fire regimes. Only certain sprouter species may respond to frequent burns by having either higher basal cover percentages and/or plant densities. The differences in response of sprouter species to a fire regime may be due to differences in their vulnerability to being displaced by overstorey proteas.

CHAPTER 4 THE EFFECT OF UNDERSTOREY SPROUTING SPECIES ON ALPHA DIVERSITY LEVELS OF MOUNTAIN FYNBOS SPECIES.

4.1 Introduction

Species richness of fynbos communities declines where repeated short-cycle fires eliminate the overstorey proteas (Chapter 2). Such changes in the species richness of fynbos areas may well be due to altered competitive interactions between overstorey proteas and sprouting understorey species. I have shown that the basal cover of understorey sprouters may increase up to 32% in frequently burned areas where the overstorey proteas have been repeatedly absent (Chapter 3). Furthermore, I will show in Chapter 5 that overstorey proteas are able to curb the vegetative growth and seed production of understorey sprouters. As sprouters may have a competitive advantage over non-sprouting species in the first few years after a fire (Bell *et al* 1987), increases in the basal cover of sprouters can reduce the number of post-fire regeneration "gaps" available to other species. The local dominance of certain sprouters may prevent many non-sprouting species from establishing after fires. This dominance may result in lower species richness of fynbos communities at such sites. The aim of this chapter is to determine; (i) if high basal cover percentages of understorey sprouters affects the α-diversity values of understorey species and (ii) whether certain guilds of understorey species are displaced by dense tussocks of understorey sprouters.

4.2 Study Site

Data for this study were collected in an area of approximately 200m X 100m at study Site One. A detailed description of study Site One is given in Chapter 1 and its fire history is summarized again in Table 4.1. The vegetation was 2 years-old when the data were collected in 1995. In the previous fire-cycle the overstorey proteas did not form a complete overstorey canopy in the area. Understorey sprouters occurred mostly as clumps of intermixed species, rather than single species tussocks, but *Tetraria ustulata* was a common component in these mixed tussocks of sprouting species.

TABLE 4.1: Fire history of study Site One. (Data determined from unpublished management records of the Swartberg Nature Reserve, Cape Nature Conservation).

Date of last fire - November 1993
Age of vegetation with last fire - 13 years
Preceding fire frequency - 13 years

4.3 Methods

I compared the α-diversity levels (number of species per quadrat) and frequency of different understorey species in three different micro-habitats to determine if high basal cover percentages of understorey sprouters could displace other understorey species. These micro-habitats were; (i) within clumps of understorey sprouting species, (ii) in the open and (iii) under the canopy of a burned overstorey proteoid shrub.

As clumps of understorey sprouters tended to be an heterogeneous species mix, no single understorey sprouting species could be used in this study. The basal area of clumps of understorey sprouters rarely exceeded an area of 0.25-m^2, which limited the quadrat size that could be used to determine α-diversity levels to 0.25-m^2.

Data were collected by locating quadrats at random along transects through the study area. The criteria for the quadrats were: (i) for the "In Sprouter" quadrats, that more than 80% of a quadrat should be filled with the basal cover of understorey sprouters and no burned overstorey proteas were present in the previous fire-cycle; (ii) for the "In Open" quadrats, that no burned canopy of overstorey proteoid shrub should be present and with less than 25% cover for any understorey sprouting species; and (iii) for the "Under Protea" quadrats, that the overstorey proteas should have had a 100% canopy cover in the previous fire-cycle. Any quadrats which did not correspond to these criteria or had $\geq$ 25% of the surface area covered with surface rock cover were not sampled. I continued to sample quadrats along the transects until 30 quadrats were found for each of three types of microhabitats.

All the species present in each quadrat were recorded and mean α-diversity and standard error values were determined from the 30 samples for each of the micro-habitat types. Because sample sizes were large, significance differences between the

three micro-habitats were determined by means of a One-Way Analysis of Variance test and Tukey's Multiple Range Test (Zar 1984). The data were analyzed not only for the total number of understorey species present in quadrats but also for the number of species recorded in the following species guilds; (i) understorey non-sprouters, (ii) understorey sprouters, (iii) short-lived understorey species (species which have a maximum life-span of 10 years) and (iv) long-lived understorey species (species whose life-span exceeds 10 years).

The number of times which the more abundant individual species, those observed in ≥ 15 quadrats (to render expected occurrence under a null hypothesis as ≥ 5 in each micro-habitat type), occurred in the micro-habitat types were compared by means of a "Goodness-of-fit" Chi-square test (Siegel & Castellan 1988). Where significant differences were found in the occurrence of a species in the three micro-habitats the data were partitioned, following the protocol of Siegel & Castellan (1988), to determine where the differences lay.

4.4 Results

In dense clumps of sprouting species the mean number of understorey species was significantly less than those in the open and under the burned skeletons of overstorey proteas ($P < 0.001$; Table 4.2). The mean number of species in the different guilds of species followed a similar trend, with significantly

less non-sprouting, short- and long-lived understorey species in dense clumps of understorey sprouters than in the open or under the burned overstorey proteas ($P < 0.001$; Tables 4.2). However, the mean number of sprouting species were as high in dense clumps of sprouters as they were in the "In Open" micro-habitat. Significantly more sprouting species occurred in quadrats located under the burned overstorey proteoid shrubs than in the dense clumps of the understorey sprouters ($P < 0.001$; Table 4.2).

Table 4.2: Mean number of all understorey species and those in different guilds of understorey species in three different micro-habitat types. Data sampled in 2-year-old mountain fynbos from 30 randomly located 0.5 X 0.5m quadrats in each of the micro-habitat types with; "In Sprouter" = in dense clumps of understorey sprouters with ≥ 80% of quadrat filled with basal cover of understorey sprouting species; In Open = in the open with ≤ 25% of quadrat filled with basal cover of understorey sprouters; Under Protea = underneath the burned canopy of overstorey protea shrubs with any percentage of basal cover of understorey sprouters. (Standard errors in parentheses; different superscripts in a row indicate significant differences at $P < 0.01$.)

	IN SPROUTER	IN OPEN	UNDER PROTEA
SPROUTERS	3.5 (0.22)^{a}	4.8 (0.40)^{ab}	5.2 (0.39)^{b}
NON-SPROUTERS	2.2 (0.33)^{a}	6.9 (0.51)^{b}	8.3 (0.49)^{b}
SHORT-LIVED	1.8 (0.30)^{a}	5.0 (0.38)^{b}	5.9 (0.44)^{b}
LONG-LIVED	3.9 (0.25)^{a}	6.7 (0.43)^{b}	7.5 (0.46)^{b}
ALL SPECIES	5.7 (0.44)^{a}	12.2 (0.67)^{b}	14.0 (0.66)^{b}

None of the species which occurred in the dense clumps of understorey sprouters were exclusive to this micro-habitat. Several species were only encountered in the "In Open" and/or in the "Under Protea" micro-habitats. Of the 55 understorey species encountered in this study, 33 species occurred in all three micro-habitat types, while 5 species were exclusive to each of the "In Open" and "Under Protea" micro-habitats (Table 4.3).

Table 4.3: Number of understorey species exclusive to a micro-habitat type (in bold), the number of species shared between micro-habitat types and total number of species encountered in 2-year old mountain fynbos. Data from 30 randomly located 0.25-m² quadrats in each micro-habitat type. "In Sprouter" = in dense clumps of understorey sprouters with ≥ 80% of quadrat filled with basal cover of understorey sprouting species; In Open = in the open with ≤ 25% of quadrat filled with basal cover of understorey sprouters; Under Protea = underneath the burned canopy of overstorey protea shrubs with any percentage of basal cover of understorey sprouters.

	NUMBER OF SPECIES		
MICRO-HABITAT	IN SPROUTER	IN OPEN	UNDER PROTEA
IN SPROUTER	**0**	0	1
IN OPEN	0	**5**	11
UNDER PROTEA	1	11	**5**
TOTAL NUMBER OF SPECIES	34	49	50

Species which were either equally frequent in all three habitat types, or which were absent in the dense clumps of

understorey sprouters, did not belong to any specific guild of understorey species. Species which were equally frequent in all three habitat types included short-lived herbs (*e.g. Centella affinis* and *Phyllopodium elegans*), geophytes (*e.g. Romulea atrandra*), myrmecochorous graminoids (e.g. *Caesia contorta*) and myrmecochorous sprouting shrublets (*e.g. Agathosma capensis*). Those species, which were less frequent or absent in the dense clumps of sprouters, also included short lived-herbs (*e.g. Indigofera heterophylla*, *Pelargonium ovale* and *Ursinea anthemoides*), myrmecochorous graminoid species (*e.g. Hypodiscus albo-aristatus*), myrmecochorous shrublets (*e.g. Polygala garcinii*) and long-lived shrubs (*e.g. Metalasia massonii*).

4.5 Discussion

Where understorey sprouters have high basal cover percentages they displace many other species. In quadrats located where sprouters had high basal cover percentages (> 80 %), the mean number of understorey species was less than half those recorded from quadrats where sprouters were sparse (< 25 % basal cover). In dense clumps of sprouters the number of understorey sprouter species is not lower, but many short- or long-lived non-sprouting species are unable to persist where sprouters have high basal cover percentages. *Tetraria ustulata* was the most common understorey sprouter in dense clumps of understorey sprouters in this study, but several other understorey sprouting species usually co-occurred with it. Even at the

relatively small scale of 0.25-m^2, understorey sprouters tended to form heterogeneous species clumps where several sprouting species co-occurred. It is thus not possible to ascribe the competitive ability of understorey sprouters to a single sprouter species in this study.

Results from this study support those of Chapter 2. Even at the small spatial scale of 0.25-m^2, the mean number of understorey species under the burned proteas did not differ from those located in the open where the sprouters were sparse. However, the mean number of understorey species under the burned overstorey proteas were more than double those of quadrants located in the dense clumps of sprouters. In Chapter 5, I will show that these overstorey protea shrubs are able to suppress certain aggressive understorey sprouters from re-establishing rapidly and gaining local dominance at a site after a fire. This can explain why even the α-diversity of sprouter species was much higher under the burned overstorey proteas than in the dense clumps of sprouters. The reduced competitive ability of some sprouters, due to the pre-fire presence of overstorey proteas, not only enables more sprouter species to co-occur but also more other understorey species to coexist.

No one species was restricted to the "In Sprouter" habitat. Several species were restricted to the "In Open" and "Under Protea" micro-habitats. Sites under burned proteas and

in the open, where sprouters are sparse, seem to represent distinct safe establishment sites for certain understorey species. No specific guild of understorey species seem to be restricted to the "In Open" or the "Under Protea" micro-habitats. Thus habitat preferences seem to be species specific. Approximately 35% of the understorey species encountered in this study did not occur in the dense clumps of sprouters. These results indicate that the local basal cover density of understorey sprouters affect the availability of post-fire regeneration gaps for species, which in turn determines the α-diversity levels in fynbos communities.

4.6 Conclusions

1. Clumps of understorey sprouters with high basal cover percentages are able to displace many understorey species. The α-diversity of understorey species can be more than 50% less where sprouters have high basal cover percentages than where they have low basal cover percentages.

2. In this study, no one specific species or guild of species were restricted to the dense clumps of sprouters. Several species were restricted to establishment sites in the open where the sprouters were sparse and under the burned canopies of overstorey proteas. The total number of understorey species in areas where sprouters have high

densities and/or basal cover percentages will thus be fewer than where they are sparse.

CHAPTER 5: COMPETITIVE INTERACTIONS BETWEEN OVERSTOREY PROTEAS AND SPROUTING UNDERSTOREY SPECIES.

5.1 Introduction

What mechanisms lead to the results obtained in this study? I hypothesize that competitive interactions between species affect the species richness of these communities, as has been shown to be the case in many other communities (*e.g.* Rosenzweig 1995 and references therein). Such competitive interactions have rarely been studied in the fynbos vegetation. However, fynbos overstorey species may compete vigorously with each other for space, with the outcome of such competition determined by the prevalent fire (disturbance) regime (Yeaton & Bond 1991). High densities of overstorey species may also displace many understorey species in Mediterranean-type shrublands, but the outcome of such competition also depends on the prevalent fire regime (Cowling & Gxaba 1990; Keith & Bradstock 1994). Previous results of this study indicated that high densities of overstorey proteas may enhance, and not reduce, the species richness of understorey species and that the basal cover percentage of understorey sprouters may increase where several short fire-cycles have eliminated the overstorey proteas (Chapters 2&3).

In this chapter I investigate competitive interactions between overstorey proteas and understorey sprouters at several pyric successional stages of a fynbos community. I hypothesize

that understorey sprouters suppress the seedling establishment and growth of overstorey proteas in the first few years after a fire, but that once the overstorey proteas manage to form an overstorey canopy over the understorey sprouters, they are able to suppress the growth and fecundity of understorey sprouters. Null hypotheses are;

(i) post-fire seedling establishment of overstorey proteas is not significantly affected by sprouting understorey species.

(ii) during the inter-fire period, understorey sprouters have no significant effect on the growth rate and reproduction of overstorey proteas.

(iii) an overstorey canopy of proteoid shrubs has no significant effect on the vegetative growth and fecundity of understorey sprouters during the inter-fire period.

(iv) the pre-fire presence of an overstorey canopy of proteoid shrubs has no significant effect on the post-fire vegetative growth and fecundity of understorey sprouters.

5.2 Study site

The above mentioned hypotheses required that data had to be collected in a fynbos community at different pyric successional stages. Six study sites which differed only in their age since the last fire were selected. These sites are study sites 1,3,4,5,6 & 7, which are described in more detail in Chapter 1. Here I will briefly summarize the relevant information for each study site which are necessary to interpret the data obtained to answer the questions posed above.

5.2.1 Effect of sprouters on protea seedling establishment

Data to investigate the competitive effect of sprouting understorey species on seedling establishment of overstorey proteas were collected from Sites One & Three where the fynbos was burned recently and the protea seedlings were 2-3-years old. At this stage after a fire all the overstorey protea seedlings have established and mortalities of seedlings, which may occur in the first summer after establishment, have taken place (Kruger 1983; Midgley 1988). The fire histories and state of the overstorey proteas when burned are summarized in Table 5.1.

TABLE 5.1: Fire histories and age of vegetation when data were collected from study Sites One and Three. (Data determined from unpublished management records of the Swartberg Nature Reserve, Cape Nature Conservation, unpublished records).

	SITE 1	SITE 3
Date of last fire:	November 1993	February 1992
Age of vegetation when burned:	13 years	13 years
Height of proteas when burned:	1.5-1.8m	1.2-1.5m
Number of times Proteas flowered when burned:	2nd-3rd time	3rd-4th time
Age of vegetation when sampled:	2 years	3 years

Two adjacent sub-sites were sampled at Site Three, but only one area at Site One. The sites were selected to have *Protea eximia*, *Protea lorifolia* and *Protea repens* present as overstorey protea species and *Cannamois scirpoides*, *Leucadendron salignum* and *Tetraria ustulata* present as understorey sprouters. At each site only one of the understorey sprouters was dominant, while the other two understorey species were present but not dominant. The effect of *Tetraria ustulata* on overstorey protea seedling establishment was investigated at Site One. The effect which *Cannamois scirpoides* and *Leucadendron salignum* have on the seedling establishment of proteoid shrubs was investigated at the two sub-sites of Site Three.

5.2.2 Effect of sprouters on growth and flowering of Proteas

Data to investigate the competitive effect of sprouting understorey species on growth and flowering of overstorey

proteas were collected from two neighboring sites, Site Four and Site Five. The fire histories and condition of the overstorey proteas when data were collected from these two sites are summarized in Table 5.2.

TABLE 5.2: Fire histories and age of vegetation when data were collected from study Sites Four and Five. (Data determined from unpublished management records of the Swartberg Nature Reserve, Cape Nature Conservation, unpublished records).

	SITE 4	SITE 5
Date of last fire:	May 1980	January 1980
Age of vegetation when burned:	10 years	20 years
Age of vegetation when sampled:	15 years	15 years
Height of proteas when sampled:	1.5-2.0m	1.5-2.0m
Number of times Proteas flowered when sampled:	3rd-4th time	3rd-4th time
Height of sampled understorey:	1.0-1.2m	1.0-1.2m

These two sites were selected to have *Protea lorifolia* and *Protea repens* present as overstorey protea species and *Cannamois scirpoides*, *Hypodiscus striatus* and *Leucadendron salignum* present as understorey sprouters. Two sub-sites were also sampled at Site Four and one area at Site Five. At each site only one of the understorey sprouters was dominant, while the other two understorey species were present but not dominant. Data to investigate the effect which *Cannamois scirpoides* and *Hypodiscus striatus* have on the fecundity of *Protea repens* and *P.lorifolia* were collected at the two sub-sites of Site Four and the data to investigate the effect which *Leucadendron salignum* has on the fecundity of *P.repens* and *P.lorifolia* were collected at Site Five.

5.2.3 Effect of protea overstorey on sprouter growth and flowering

All the data to investigate the effect of overstorey proteas on growth and flowering of understorey sprouting species were collected from study Site Five. Although both *Protea lorifolia* and *Protea repens* were abundant at Site Five, only *Protea repens* shrubs formed a well-developed overstorey canopy over *Cannamois scirpoides*, *Hypodiscus striatus* and *Leucadendron salignum* plants. I could not find a suitable study site where adequate numbers, for statistical testing, of *Protea lorifolia* formed an overstorey canopy over these three understorey resprouters. The fire history of Site Five and the condition of its vegetation when the data were collected are summarized in Table 5.2.

5.2.4 Effect of pre-fire protea overstorey on post-fire performance of sprouters

Data to investigate the effect of overstorey proteas during previous fire-cycle on the post-fire fecundity of understorey sprouters were collected from study Sites Six and Seven. The fire histories and the age of the vegetation when last burned are summarized in Table 5.3.

TABLE 5.3: Fire histories and age of vegetation when data were collected from study Sites Six and Seven. (Data determined from unpublished management records of the Swartberg Nature Reserve, Cape Nature Conservation, unpublished records).

	SITE 6	SITE 7
Date of last fire:	February 1992	November 1987
Age of vegetation when burned:	17 years	21 years
Height of proteas when burned:	1.5-2.0m	1.8-2.0m
Age of vegetation when sampled:	3 years	8 years

Although both *Protea lorifolia* and *Protea repens* were abundant at Sites Six and Seven, only *Protea repens* shrubs formed a well-developed overstorey canopy over *Cannamois scirpoides*, *Hypodiscus striatus* and *Leucadendron salignum* plants in the previous fire-cycle. Similarly to study Sites Five and Six, I could not find a study area where adequate numbers of *Protea lorifolia* formed an overstorey canopy over these understorey resprouters. The data to investigate the effect which a pre-fire overstorey of *Protea repens* had on the post-fire fecundity of *Cannamois scirpoides* and *Hypodiscus striatus* were collected at Site Six and the pre-fire overstorey canopy effect of *P.repens* on *Leucadendron salignum* data were collected at study Site Seven.

5.3 Methods

5.3.1 Effect of sprouters on protea seedling establishment

To determine whether proteoid seedling establishment is affected by sprouting understorey species, I compared the number of quadrats in which proteoid seedlings occurred from 100 0.5 X 0.5m quadrats in each of the following three micro-habitats; (i) under the canopy of a burned overstorey proteoid shrub, (ii) in the open and (iii) < 0.1m from the most abundant understorey resprouting species at a site. The quadrats were randomly located along a 300-500m transect through each site, where the overstorey proteas were of a similar density (1000-2500 plants per ha) in the previous fire-cycle. The number and species of proteoid seedlings in a quadrat were recorded as "Under Protea" where a quadrat fell under the burned canopy skeleton of a proteoid shrub, as "In Open" where a quadrat fell in the open with no proteoid shrub present and with < 25% cover of any understorey sprouting species in the quadrat and as "In Sprouter" where ≥ 80% of a quadrat was filled with the basal cover of the most abundant understorey sprouting species of the site. Quadrats which fell in areas with ≥ 50% surface rock cover were ignored. I continued to sample quadrats along the transect until 100 quadrats, which conformed to the above categories were obtained for each of the three micro-habitat types. This protocol was followed for three sites. At each site a different understorey species was most abundant. The

understorey sprouting species which were most abundant at a site were *Tetraria ustulata* (Cyperaceae), *Cannamois scirpoides* (Restionaceae) and *Leucadendron salignum* (Proteaceae).

At all three sites, *Protea eximia*, *P. lorifolia* and *P. repens* were present as overstorey proteas. The observed versus expected number of times seedlings of these three overstorey species occurred within the 100 quadrants were compared for each site by means of a Chi-square test for 3X3 tables, with the number of times seedlings of *Protea eximia*, *P. lorifolia* and *P. repens* were recorded in quadrats as row heading and with "Under Protea", "In Open" and "In Sprouter" micro-habitats as column headings (Siegel & Castellan 1988). For each site in which the three overstorey species did not differ in their pattern of seedling establishment in the three micro-habitats, the seedling data of the three overstorey proteoid species were lumped as a single species guild (overstorey proteas) and compared for each micro-habitat by means of a "Goodness-of-fit" Chi-square test (Siegel & Castellan 1988). I assumed that the null hypothesis would be that an equal number of quadrats with protea seedlings would be found in each of the three micro-habitat types. Where significant ($P < 0.05$) differences were found between seedling frequencies in the three micro-habitats the data were partitioned between "Under Protea" versus "In Open + In Sprouter", and "In Sprouter" versus "In Open" seedling frequencies. These Chi-square tables were analyzed to

see where differences occurred following the protocol of Siegel & Castellan (1988).

5.3.2 Effect of sprouters on growth and flowering of Proteas

The effect which sprouting understorey species have on the growth and flowering of overstorey proteas during the inter-fire period was investigated by means of comparing the flower production of proteoid shrubs which grew within the basal cover area of an understorey sprouter with those of plants which were growing in the open. I assumed that the juvenile period (number of years to first flower) would reflect the growth rate while the annual number of inflorescences produced by an overstorey proteoid shrub would reflect fecundity of a plant. Thus, I assumed that a difference in juvenile period and annual flower production of proteoid shrubs, which grew in the open versus those which grew within an understorey sprouter, would indicate the extent to which competition from the understorey species affected the fecundity of the overstorey proteoid shrubs.

I investigated the effect which two resprouting restioid species, *Cannamois scirpoides* and *Hypodiscus striatus*, and one resprouting shrub species, *Leucadendron salignum*, had on the fecundities of two overstorey proteas, *Protea repens* and *P.lorifolia*. For each understorey-overstorey species pair I located an overstorey proteoid shrub which was growing within 0.3m of the base of a *Leucadendron salignum* plant, or within

the basal cover area of *Cannamois scirpoides* and *Hypodiscus striatus*. Such overstorey proteas were regarded as growing within a sprouter. The number of years a shrub flowered since establishment (called Years Flowering in the tables) and the number of inflorescences it produced during the last flowering season were recorded for *Protea repens*. For *Protea lorifolia* the number of years an individual flowered and the total number of inflorescences on an individual were recorded, because inflorescences persist for many years in this species and the total number of flowers an individual plant produced can be recorded accurately. For each overstorey protea growing in a sprouter which I sampled, I located the closest (< 5m away) proteoid shrub growing in the open and recorded similar data from it. I operationally defined growing in the open as growing at least 0.5m from any of the two understorey restioid species and at least 1.0m away from a *Leucadendron salignum* plant. For each understorey resprouter-overstorey protea species pair, 30 samples were collected. Means and standard errors were calculated for the number of years until shrubs first flowered (juvenile phase) and the flower production of the proteoid shrubs growing in an understorey sprouter and in the open. Statistical analysis were done by using the Wilcoxon-Signed-Ranks test to determine if paired samples of plants, those growing in sprouters *versus* those growing in the open, differed in the number of years they have flowered and/or the number of flowers they produced (Siegel & Castellan 1988).

5.3.3 Effect of protea overstorey on sprouter growth and flowering

To determine the effect of an overstorey canopy on understorey sprouting species during the inter-fire period, I compared the vegetative growth and annual seed production of plants of the understorey sprouters *Cannamois scirpoides*, *Hypodiscus striatus* and *Leucadendron salignum* which grew under the canopy of *Protea repens* shrubs versus those of plants which grew in the open. I defined vegetative growth as the number of culms produced on a rhizome during the last year for *Cannamois scirpoides* and *Hypodiscus striatus* and for *Leucadendron salignum* as the total number of stems on an individual bearing inflorescences.

To collect the data for the two restioid understorey sprouters, *Cannamois scirpoides* and *Hypodiscus striatus*, I sampled 30 individuals of each of these species growing within 0.3m from the base of a *Protea repens* shrub. I excavated these tussocks and, at random, selected one intact rhizome per tussock. Next I counted the number of culms and total number of seed produced in the last year for each rhizome. I also sampled 30 randomly selected plants of *Leucadendron salignum* which grew within 0.3m from the stem of the closest *Protea repens* shrub and counted the number of stems which were bearing inflorescences and the total number of inflorescences produced during the last flowering season. These data were paired with data collected from 30 individuals which grew in the open, at a

distance greater than 1.0m from base of each *Protea repens* plant. Statistical significance of differences in values for understorey plants, which grew under the canopy of *Protea repens* shrubs versus those of plants which grew in the open, were determined by using the Wilcoxon-Signed-Ranks test (Siegel & Castellan 1988).

5.3.4 Effect of pre-fire Protea overstorey on post-fire performance of sprouters

A similar procedure to those described in section 5.3.3 was followed to test the effect of overstorey proteas on the regrowth of understorey sprouter species after a fire. The only difference in procedure being that I collected the data in the post-fire environment from *Cannamois scirpoides*, *Hypodiscus striatus* and *Leucadendron salignum* plants which grew under the canopy of *Protea repens* shrubs and those of plants which grew in the open (> 1.0m from base of *P.repens*) during the previous fire-cycle. The post-fire fecundity of understorey plants which grew under an overstorey canopy of *P.repens* were compared with those of plants which grew in the open in the previous fire-cycle. Care was taken to sample only understorey plants which established at least 1.0m away from an overstorey shrub in the post-fire environment, to ensure that the post-fire fecundity of understorey plants was not affected by the presence of an overstorey in the current fire-cycle.

5.4 Results

5.4.1 Effect of sprouters on Protea seedling establishment

The three overstorey species, *Protea eximia*, *Protea lorifolia* and *Protea eximia* were similar in their pattern of seedling establishment in the different micro-habitats. No significant differences were found between the three overstorey species in their preference of establishment in the three micro-habitats at the site where the understorey sprouter *Tetraria ustulata* was dominant ($P > 0.8$; Table 5.1), the site where *Cannamois scirpoides* was dominant ($P > 0.3$; Table 5.2) and the site where *Leucadendron salignum* was the most common sprouter ($P > 0.3$; Table 5.3). However, significant differences were found in the tendency of the protea seedlings to establish in the three micro-habitat types when all the protea species were treated as one. A significantly higher number of the quadrats located under the burned overstorey proteas had proteoid seedlings in them than quadrats located in the open and quadrats located near sprouters for the site where *Tetraria ustulata* was the dominant sprouter ($P < 0.001$; Table 5.1), the site where *Cannamois scirpoides* was dominant ($P < 0.02$; Table 5.2) and at the site where *Leucadendron salignum* was the dominant sprouter ($P < 0.01$; Table 5.3).

Table 5.1: Number of quadrats in which seedlings of *Protea eximia*, *Protea lorifolia* and *Protea repens* established in 2-year-old mountain fynbos at study Site One, where *Tetraria ustulata* was the most abundant understorey resprouter. Data for 100 quadrats of 0.25-m² in each of three different micro-habitats, defined as; "Under Protea" = under burned canopy of overstorey proteoid shrubs; "In Open" = where no proteoid shrub occurred in the previous fire-cycle and where quadrat was filled with < 25% basal cover of any understorey sprouting species; "In Sprouter" = ≥ 80% of quadrat filled with the basal cover of the most abundant sprouting species at a site.

	UNDER PROTEA	IN OPEN	IN SPROUTER
Protea eximia	33	23	7
Protea lorifolia	6	5	0
Protea repens	11	6	2
QUADRATS WITH PROTEA SEEDLINGS	50	34	9

Table 5.2: Number of quadrats in which seedlings of *Protea eximia*, *Protea lorifolia* and *Protea repens* established in 3-year-old mountain fynbos at study Site Three, where *Cannamois scirpoides* was the most abundant understorey resprouter. Data collected and micro-habitat definitions as in Table 5.1.

	UNDER PROTEA	IN OPEN	IN SPROUTER
Protea eximia	31	10	10
Protea lorifolia	22	17	13
Protea repens	7	6	5
QUADRATS WITH PROTEA SEEDLINGS	47	27	26

Table 5.3: Number of quadrats in which seedlings of *Protea eximia*, *Protea lorifolia* and *Protea repens* established in 3-year-old mountain fynbos at study Site Three, where *Leucadendron salignum* was the most abundant understorey resprouter. Data collected and micro-habitat definitions as in Table 5.1.

	UNDER PROTEA	IN OPEN	IN SPROUTER
Protea eximia	18	14	5
Protea lorifolia	22	17	10
Protea repens	3	9	4
QUADRATS WITH PROTEA SEEDLINGS	42	28	16

In a comparison of the number of quadrats in which protea seedlings occurred, for quadrats located in the open *versus* quadrats located near a sprouter, I noted that not all sprouter species have a similar affect on the seedling establishment of the overstorey proteas. A significantly higher number of quadrats located in the open contained seedlings, than quadrats located near *Tetraria ustulata* ($P < 0.001$; Table 5.1), but the number of quadrats which contained protea seedlings did not differ significantly for quadrats located in the open and those located near *Cannamois scirpoides* and *Leucadendron salignum* (Tables 5.2 & 5.3). The post-fire seedling establishment of overstorey proteas may thus only be affected by understorey resprouting species such as *Tetraria ustulata* and not by all understorey sprouter species.

5.4.2 Effect of sprouter on growth and flowering of Protea

The flower production and number of years to first flowering of *Protea repens* and *P.lorifolia* plants can be affected by the presence of some, but not all, understorey resprouters. Where *Protea repens* and *Protea lorifolia* plants established near *Cannamois scirpoides* tussocks the number of years they flowered and their flower production were significantly lower than those of plants which established in the open ($P < 0.001$; Table 5.4). However, the number of years to first flowering and annual flower production of *Protea repens* were not significantly affected where they establish in tussocks of *Hypodiscus striatus* (Table 5.5). However, where *Protea lorifolia* plants established in *Hypodiscus striatus* tussocks, the number of years they flowered and their total flower production were significantly lower than those of plants which established in the open ($P < 0.001$; Table 5.5). The resprouting shrub *Leucadendron salignum* had a similar affect on *Protea repens* and *P.lorifolia*, with the number of years the *Protea* plants flowered and their flower production significantly lower in plants which established within 0.3m of *Leucadendron salignum*, than those of plants which established in the open ($P < 0.001$; Table 5.6).

Table 5.4: Means and standard errors (in parentheses) for number of years flowering and flower production of 14-year-old *Protea repens* and *Protea lorifolia* plants growing within the resprouter *Cannamois scirpoides* and in the open. Data from 30 paired random samples of number of flowers produced during last flowering season for *P.repens* and total number of flowers on *P.lorifolia* plants growing within a *Cannamois* tussock (In Sprouter) and more than 1 m away from a *Cannamois* tussock (In Open).

		YEARS FLOWERING	FLOWERS PRODUCED
Protea repens	IN SPROUTER	2.3 (0.28)	11.3 (2.26)
Protea repens	IN OPEN	4.8 (0.26)	74.0 (8.54)
Protea lorifolia	IN SPROUTER	1.7 (0.22)	5.8 (1.45)
Protea lorifolia	IN OPEN	3.4 (0.16)	29.1 (3.21)

Table 5.5: Means and standard errors (in parentheses) for number of years flowering and flower production of 14-year-old *Protea repens* and *Protea lorifolia* plants growing within the resprouter *Hypodiscus striatus* and in the open. Data from 30 paired random samples of number of flowers produced during last flowering season for *P.repens* and total number of flowers on *P.lorifolia* plants growing within a *Hypodiscus* tussock (In Sprouter) and more than 1m away from a *Hypodiscus* tussock (In Open).

		YEARS FLOWERING	FLOWERS PRODUCED
Protea repens	IN SPROUTER	3.8 (0.30)	37.6 (6.04)
Protea repens	IN OPEN	4.1 (0.36)	39.7 (6.67)
Protea lorifolia	IN SPROUTER	1.5 (0.19)	4.1 (1.10)
Protea lorifolia	IN OPEN	3.4 (0.17)	29.4 (3.03)

Table 5.6: Means and standard errors (in parentheses) for number of years flowering and flower production of 15-year-old *Protea repens* and *Protea lorifolia* plants growing within the resprouter *Leucadendron salignum* and in the open. Data from 30 paired random samples of number of flowers produced during last flowering season for *P.repens* and total number of flowers on *P.lorifolia* plants growing within 0.3m from a *Leucadendron* plant (In Sprouter) and more than 1 m away from a *Leucadendron* plant (In Open).

		YEARS FLOWERING	FLOWERS PRODUCED
Protea repens	IN SPROUTER	3.3 (0.22)	18.8 (2.40)
Protea repens	IN OPEN	4.7 (0.16)	47.4 (4.55)
Protea lorifolia	IN SPROUTER	1.4 (0.22)	5.2 (1.69)
Protea lorifolia	IN OPEN	2.7 (0.18)	19.1 (2.09)

5.4.3 Effect of overstorey proteas on sprouter growth and flowering.

Initially the presence of an understorey sprouter can affect the growth and flower production of the overstorey proteas (Section 5.4.2), but the competitive effect is reversed once the proteoid shrubs develop an overstorey canopy over the understorey sprouters. The number of culms and the number of seed produced per rhizome of *Cannamois scirpoides* plants, which grew under 15-year-old *Protea repens* plants, were significantly lower than those of plants which grew in the open ($P < 0.001$; Table 5.7 & Figure 5.1). *Hypodiscus striatus* followed a similar pattern, with significantly fewer culms ($P < 0.05$) and seed ($P < 0.001$) per rhizome for plants growing under *Protea repens* shrubs than those of plants growing in the open (Table 5.8).

FIGURE 5.1: Effect of an overstorey of *Protea repens* on the annual growth and seed production of the understorey sprouter *Cannamois scirpoides*. The plant to the left of the 1m measuring-rod grew in the open, whilst the plant on right grew under a 15-year-old *P. repens* shrub. The excavated rhizome of each *C.scirpoides* plant display all the culms and inflorescences produced during the last year.

The resprouting shrub *Leucadendron salignum* also followed this pattern, with plants growing under *Protea repens* having significantly fewer flower bearing stems ($P < 0.05$) and their annual inflorescence production lower ($P < 0.001$), than those of plants growing in the open (Table 5.9).

Table 5.7: Means and standard errors (in parentheses) for annual number of culms and seed *Cannamois scirpoides* produced per rhizome, for plants growing under 15-year old *Protea repens* shrubs and those growing in the open. Data from 30 paired random samples of plants growing within 0.3m from the base of a *P.repens* shrub (Under Protea) *versus* those which grew > 1m from the base of a *P.repens* plant (In Open).

	NUMBER OF CULMS	NUMBER OF SEED
UNDER PROTEA	2.4 (0.18)	8.1 (1.12)
IN OPEN	5.7 (0.44)	23.7 (2.32)

Table 5.8: Means and standard errors (in parentheses) for annual number of culms and seed *Hypodiscus striatus* produced per rhizome, for plants growing under 15-year old *Protea repens* shrubs and those growing in the open. Data from 30 paired random samples of plants growing within 0.3m from the base of a *P.repens* shrub (Under Protea) *versus* those which grew > 1m from the base of a *P.repens* plant (In Open).

	NUMBER OF CULMS	NUMBER OF SEED
UNDER PROTEA	5.3 (0.32)	2.1 (0.29)
IN OPEN	6.6 (0.62)	6.3 (0.65)

Table 5.9: Means and standard errors (in parentheses) for number of flower bearing stems and number of inflorescences produced on *Leucadendron salignum* plants growing within 0.3m from a *Protea repens* shrub (Under Protea) and those which grew > 1m from the base of a *P.repens* plant (In Open).

	NUMBER OF STEMS	NUMBER OF INFLORESCENCES
UNDER PROTEA	3.6 (0.36)	24.0 (3.05)
IN OPEN	4.7 (0.46)	72.7 (9.37)

5.4.4. Effect of overstorey proteas on post-fire performance of sprouters

An overstorey canopy of *Protea repens* may not only affect the growth and fecundity of understorey sprouters during the inter-fire period (Section 5.4.3) but also their performance after a fire. However, an overstorey of *Protea repens* in one fire-cycle does not affect the post-fire performance of all understorey resprouting species equally. Three years after a fire the total number of culms and seed produced per rhizome of *Cannamois scirpoides* plants which grew under 17-year-old *Protea repens* plants in the previous fire-cycle, were significantly lower than those of plants which grew in the open ($P < 0.001$; Table 5.10). In *Hypodiscus striatus* the number of culms produced per rhizome in the last 3 years since the fire were also significantly lower in plants which grew under *Protea repens* plants in the previous fire-cycle than those of plants which grew in the open ($P < 0.001$; Table 5.11), but the number of seed produced per rhizome did not differ between plants which

grew under *Protea repens* and in the open (Table 5.11). Even 8 years after a fire the performance of *Leucadendron salignum* plants which grew under the canopy of *P.repens* in the previous fire-cycle, was lower than those of plants which grew in the open (Table 5.12). *Leucadendron salignum* plants which grew under 21-year old *Protea repens* plants in the previous fire-cycle had significantly fewer flower bearing stems per plant and they produced fewer inflorescences per plant in the last year than plants which grew in the open in the previous fire-cycle ($P < 0.001$; Table 5.12)

Table 5.10: Post-fire performance of *Cannamois scirpoides* plants which grew under the canopy of 17-year-old *Protea repens* shrubs in the previous fire-cycle, versus those which grew in the open. Data were collected 3 years after fire, from 30 randomly selected plants. Values indicate mean number of culms or seed produced per rhizome in last 3 years since fire, with standard error values in parentheses.

	NUMBER OF CULMS	NUMBER OF SEED
UNDER PROTEA	3.6 (0.41)	6.6 (1.04)
IN OPEN	8.7 (0.88)	26.8 (3.38)

Table 5.11: Post-fire performance of *Hypodiscus striatus* plants which grew under the canopy of 17-year-old *Protea repens* shrubs in the previous fire-cycle, versus those which grew in the open. Data were collected 3 years after fire, from 30 randomly selected plants. Values indicate mean number of culms or seed produced per rhizome in last 3 years since fire, with standard error values in parentheses.

	NUMBER OF CULMS	NUMBER OF SEED
UNDER PROTEA	7.1 (0.66)	2.5 (0.44)
IN OPEN	13.0 (1.26)	4.2 (0.61)

Table 5.12: Post-fire performance of *Leucadendron salignum* plants which grew under the canopy of 21-year-old *Protea repens* shrubs in the previous fire-cycle, versus those which grew in the open. Data were collected 8 years after fire from 30 randomly selected plants. Values indicate mean number of flower bearing stems per plant and number of inflorescences produced during last year, with standard error values in parentheses.

	NUMBER OF STEMS	NUMBER OF INFLORESCENCES
UNDER PROTEA	2.5 (0.45)	13.0 (3.46)
IN OPEN	5.1 (0.69)	41.8 (6.93)

5.5 Discussion

Competitive interactions between sprouting understorey and non-sprouting overstorey species are evident in several of the pyric successional stages of the fynbos vegetation. In the initial post-fire environment, seedlings of overstorey proteoid shrubs tend to establish more frequently under their burnt

parents than in the open and rarely establish near certain understorey sprouters such as *Tetraria ustulata*. The aggregation of overstorey protea seedlings under the skeletons of their burned parent plants was also found in western Cape fynbos (Yeaton & Bond 1991). This pattern of seedling establishment may in part be due to seed dispersal. Once overstorey protea seeds are released from their serotinous cones, they are wind dispersed, traveling through the air for a short distance and thereafter tumble along the soil surface until they strike some barrier (Manders 1986; Bond 1988). Some seed may end up below their burned parents, but many will tumble at least a few meters away from their parent plants (Bond 1988). As the burned remains of understorey sprouters could act equally well as barriers to trap tumbling seed, it is difficult to explain the paucity of the overstorey protea seedlings in close proximity to certain understorey sprouters. It may be due to competition from the understorey sprouters (Bell *et al* 1987), but the precise reason awaits further research in the fynbos. Whatever the cause, one aspect is clear from this pattern of seedling establishment; overstorey protea seedlings are more likely to re-establish after a fire in the space which their mature parents filled than to establish in sites where their parents were absent. This may be particularly so where certain understorey sprouters, such as *Tetraria ustulata*, are abundant.

For up to 15 years after establishment, certain understorey sprouters may inhibit the vegetative growth and fecundity of overstorey protea plants, which established in close proximity (< 1.0m) to them. In such overstorey protea plants, the period to first flowering (juvenile phase) may be extended and the annual flower production may be lower than those of plants which established in the open. However, despite the potential initial disadvantage of establishment near an understorey sprouter, some overstorey proteoid shrubs may be able to do so. Once such overstorey protea plants have been able to develop an overstorey canopy over the understorey sprouter, they are able to repress their understorey competitor. This result may be strengthened in the next fire-cycle. The post-fire fecundity of understorey sprouters may be considerably reduced for up to 8 years after a fire if these plants had grown under the canopy of overstorey proteas in the previous fire-cycle.

The outcome of competitive interactions between overstorey proteas and sprouting understorey species will largely depend on the local fire regime. Where fire-cycles are long enough to allow overstorey proteas to establish and form well-developed canopies over the understorey species, these shrubs may be able to displace some understorey sprouters. In contrast, where fire-cycles are so short that the overstorey proteas are not able to grow taller than the understorey species, the understorey sprouters will be favoured. Where the understorey

sprouters have been favoured by several short fire-cycles, to the extent that they have high basal cover percentages, the sprouters will be able to suppress the seedling establishment, subsequent growth and fecundity of the overstorey proteas. Many of the results of this study seem to support a model presented to predict the outcome of competition between grassland species, where the initial competitive advantage of one species is temporary and relevant for competition for light (Wilson 1988). In Wilson's model the winner in the competition for light may only have a temporary advantage, because another taller species may establish next to the temporary winner, which can "outshade" it in a later pyric successional stage or in the following fire-cycle. Similarly in this study, in the competition for space, a taller plant (the overstorey proteas) may establish next to a shorter understorey sprouter and could "outshade" it later in the fire-cycle. In the fynbos the displacement of understorey species by overstorey species may only be temporary, because the overstorey proteas are slow to mature. As the overstorey proteas are slow maturing, they will always leave an initial post-fire window in which the understorey species may be able to dominate. However, as overstorey proteas can retain a competitive edge from one fire-cycle to the next fire-cycle, it stands to reason that the recurrent dominance of overstorey proteas could result in the local extinction of some sprouting understorey species with a consequent loss of local species richness (Cowling & Gxaba 1990; Keith & Bradstock 1994). Here, repeated dominance of

overstorey species may result in an inverse relationship between overstorey cover and understorey species richness (Specht & Specht 1989). Many such examples are available for the fynbos vegetation, where persistent high densities of alien overstorey shrubs displace many indigenous understorey fynbos species (Van Wilgen & Richardson 1985).

Specific species interactions may play an important role in determining the structure and species composition of fynbos communities. For instance, an overstorey canopy of *Protea repens* in one fire-cycle can reduce the pre- and post-fire performance of *Hypodiscus striatus* tussocks, while *Hypodiscus striatus* can reduce the performance of *Protea lorifolia*, but not those of *P.repens*. These results indicate that *Protea repens* will initially be more successful than *Protea lorifolia* in its establishment at sites where *Hypodiscus striatus* is dominant. However, once *Protea repens* plants have established in such areas, they can displace *Hypodiscus striatus* plants which will enable *Protea lorifolia* to establish at such sites. This result is of particular interest because it suggests the partial dependance of one overstorey proteoid species, *Protea lorifolia*, on the presence of a trophically similar species, *Protea repens*. Here *Protea repens* reduces potential competition from the understorey species *Hypodiscus striatus*, to create safe post-fire establishment sites for *Protea lorifolia*. Intricate species-specific interactions, such as the *Protea repens-Protea lorifolia-Hypodiscus striatus* example, indicate

that much of the high species turnover rates (ß-diversity) within fynbos communities (Bond 1983) and even on a landscape level (Kruger & Taylor 1979) may in part be due to species-specific competitive interactions and not only due to edaphic heterogeneity (Tilman 1982) and steep ecological gradients in the fynbos environment (Campbell & van der Meulen 1980; Cowling *et al* 1992).

5.6 Conclusions

1. Competitive interactions between overstorey proteas and sprouting understorey species were evident in several pyric successional stages.

2. Overstorey protea seedlings established more frequently under the burned skeletons of their parent plants than in the open. Also, they rarely established in close proximity to certain understorey sprouting species. The paucity of overstorey protea seedlings near some understorey sprouter species, 2-3 years after a fire, may be due to competition from the sprouters but this remains to be shown.

3. The vegetative growth and flower production of overstorey proteas which grew near understorey sprouters were lower than those of plants which grew in the open. This effect was evident for up to the first 15 years after a fire. However, not all understorey sprouters affected the

overstorey proteas equally. Specific species interactions differed.

4. The vegetative growth and seed production of understorey sprouters, which grew under a canopy of overstorey proteas during the inter-fire period, were also lower than that of plants growing in the open.

5. The post-fire growth and seed production of understorey sprouters were significantly lower in plants, which grew under an overstorey protea canopy during the previous fire-cycle, than those of plants which grew in the open in the previous fire-cycle. Therefore, a well-developed canopy of overstorey proteas in one fire-cycle can reduce the post-fire performance of understorey resprouting species in the next fire-cycle.

6. The results of this chapter demonstrate that complex species-specific, understorey-overstorey interactions are important in the fynbos. Certain overstorey species depend on trophically similar species to reduce potential competition from understorey species for their successful establishment at a site.

CHAPTER 6: **SUMMARY AND CONCLUSIONS.**

From related previous studies I differ in one conclusion. High canopy cover densities of overstorey proteas may enhance, not reduce, the post-fire species richness of understorey species in Mediterranean-type shrublands. Why I differ from previous conclusions lies in the fact that different spatial scales of measuring α-diversity must be considered before any conclusion can be drawn on the effect which overstorey shrubs have on the species richness of a community. As overstorey proteas affect the spatial arrangement, or patchiness, of understorey species and the patchiness of species affects the species richness of a community (Rosenzweig 1995), it stands to reason that overstorey proteas will increase the species richness of a community where they contribute towards the processes leading to the patchiness of species in a community. Results of this study show that overstorey proteas do increase the patchiness of species in fynbos communities. The effect which the patchiness of species has on the **species richness of a community** cannot be measured in the small-scale quadrats used by previous workers (*e.g.* Cowling & Gxaba 1990; Keith & Bradstock 1994); it only becomes apparent in measurements from larger quadrats (Chapter 2). Results from small-scale quadrats can be used to measure the degree to which one guild of species can displace another guild of species **locally**, but care must be taken when small-scale quadrat results are extrapolated to a wider spatial scale.

In this chapter I will explain how community-wide species richness is maintained in fynbos communities through differences in the competitive displacement abilities of understorey sprouters and overstorey proteas. I will also show why the prevalent disturbance regime is important in maintaining a balance between these two opposing forces.

The importance of a disturbance regime to maintain safe recruitment sites is well known for sessile organisms such as plants and marine organisms (Lavorel *et al* 1994; Rosenzweig 1995 and references therein). Disturbance regimes are needed to create establishment sites where competition from a superior competitor is reduced or eliminated. Sprouter species can have a competitive edge over non-sprouters in the fynbos because sprouters can re-establish rapidly after a fire. Thus, they can dominate in the regeneration niche. Especially where sprouters have high basal cover percentages (Chapter 4), safe establishment sites will not be equally available spatially for seedlings of non-sprouting species. Safe establishment sites will be rare for non-sprouter species where several short-cycle fire cycles have enabled sprouters to reach high basal cover percentages. The species richness of such communities will be depauperate in number of species of non-sprouting species (Chapters 2&3). Small-scaled α-diversity values remain high at such sites because several sprouter species can coexist to form large heterogeneous species clumps (Chapters 2&3).

However, larger-scaled α-diversity values are lower where sprouters are abundant, as the steepness of a species-area curve for such sites will be lower than where the sprouters are sparse. Safe establishment sites will be rare where sprouters have high basal cover percentages, which will result in a reduction in the patchiness (within community ß-diversity) of species in a community (Chapter 2). Spatial fragmentation of clumps of sprouters is thus necessary to ensure that many safe recruitment sites are available for non-sprouting species in fynbos communities. This is the reason why overstorey proteas play an important role in maintaining the species richness of fynbos communities. They are able to suppress the pre- and post-fire performance and thus the competitive ability of understorey sprouters (Chapter 5) and thereby maintain the patchiness of understorey species in a community.

High canopy cover percentages of overstorey proteas in one fire-cycle will not reduce the species richness of a community in the following fire-cycle because species which were displaced in the previous fire-cycle can regenerate from soil-stored propagules in the following fire-cycle (Kruger 1983). Unlike sprouters, overstorey proteas will leave a post-fire recruitment window for species to establish because their seedlings need several years to mature. Overstorey proteas develop a competitive advantage only several years after a fire when they are tall enough to

form an overstorey canopy (Chapter 5). Thus, at sites where overstorey proteas have restrained the post-fire performance of sprouters, many tiny seedlings of different species can coexist, even at a small spatial scale. During the inter-fire period short-lived understorey species may displace each other as one species grows taller than the other (Wilson 1988; Tilman & Pacala 1993). This process will then generate the pyric successional stages typical of fynbos communities (Kruger 1983). However, competitive exclusion from the overstorey proteas will only become operative at the last successional stage, when they form a well-developed overstorey canopy, which can outshade understorey species. Competition from overstorey proteas in this final successional phase is thus important to prevent understorey species from developing a competitive advantage in the post-fire environment.

An independent temporal factor, the frequency of the local fire regime, is important in determining the outcome of competition between the overstorey proteas and understorey sprouters. Competitive interactions between overstorey proteas and understorey sprouters are complex. Once one guild of species have been favoured at a site, it can retain a competitive advantage into the following fire-cycle (Chapter 5). For example, where the frequency of a fire regime is long enough to allow the overstorey proteas to form an overstorey canopy over the understorey sprouters,

the post-fire performance of the sprouters will be restrained and many safe recruitment sites will be available for protea seedlings. These seedlings tend to establish best only under their burned parents where the sprouters have been repressed (Yeaton & Bond 1991; Chapter 5). A patchy spatial patterning of sprouters and overstorey proteas will develop within an area where variability in the fire regime periodically favours either sprouters or overstorey proteas. Moreover, the complex species-specific competitive interactions amongst overstorey protea species and understorey sprouter species (Chapter 5) will further enhance the spatial patterning of sprouters and proteas in an area. The availability of post-fire establishment windows for many different species thus not only depends on the productivity of a site in Mediterranean-type shrublands (Specht & Specht 1989), but also on the outcome of competitive interactions amongst overstorey and understorey species as determined by the prevalent fire regime. Where resources are freely available, competitive interactions amongst different guilds of species may collapse, as the freely available resources will enable one guild of species to become dominant in the regeneration niche. In such areas a disturbance regime may no longer be effective in maintaining a balance in the spatial patterning of species and species richness in such sites will decline.

Plant species richness may thus be sigmoidally related to plant productivity (Tilman & Pacala 1993), because where plant productivity is high, a disturbance regime will no longer be effective in preventing one guild of species from becoming dominant in the regeneration niche. Particularly interesting from the results of this study is the notion that at an intermediate plant productivity level and variance of disturbance, that the species richness of a community would peak. The reason seems to be that competitive interactions between species, under these mitigated conditions, promotes heterogeneity in safe establishment sites for many different species. The importance of maintaining heterogeneity in post-fire regeneration niches in the maintenance of species richness in Mediterranean-type shrubland communities has long been known (Grubb 1977; Kruger 1983). However, the processes which produce variability in post-fire regeneration niches have not been well understood. Results of this study show that the core of these processes lies in competitive interactions amongst the overstorey proteas and understorey sprouting species, which generate **spatio-temporal availability of regeneration niches for other species** and, thus, the **patchiness and species richness of fynbos communities.** The most attractive models which could explain the species richness of fynbos communities, are patch-occupancy models (Caswell & Cohen 1993; McLaughlin & Roughgarden 1993). Results from this study indicate that

fynbos communities may not become saturated with species (Cornell 1993) where the biotic interaction (competitive displacement) between the two major opposing forces (sprouters and non-sprouters) maintain heterogeneity in the regeneration niche. However, a fynbos community may become saturated with species where the more sessile organisms (sprouters) are favoured by repeated disturbance (short-cycle fires). Under these conditions they are able to occupy more space (regeneration gaps). Also under such disturbance regimes, the non-sprouters must disperse over longer distances to find available regeneration gaps. Unlike species in other Mediterranean-type shrublands (Lavorel *et al* 1994), this is rarely possible for fynbos species as most of them have short seed-dispersal distances (Bond & Slingsby 1983).

Fynbos researchers should take note of the importance of species-specific competitive interactions amongst fynbos species. The structure and floristic composition of many fynbos communities may be induced by dynamic species-specific interactions amongst sprouting understorey and non-sprouting overstorey species. Furthermore, in studies where α-diversity values of different fynbos areas are compared the biotic effect, which overstorey species may have on α-diversity values, should be controlled for when α-diversity is measured at a spatial scale of $\geq$ 25-m^2. In large quadrats biotic interactions influence α-diversity values, which may

confound and conceal effects of abiotic factors, such as soil nutrient status (Cowling 1983).

The results of this study have some practical implications for the management of fynbos. Two major goals of most mountain fynbos conservation areas are the maintenance of the species richness of communities and maximum deliverance of runoff water from fynbos mountain water catchment areas (Van Wilgen *et al* 1994; Bond & Van Wilgen 1996). Both of these objectives may not be realized in areas where the overstorey proteas have been eliminated. Species richness of fynbos communities will only be conserved where fynbos managers maintain fire regimes which will ensure the persistence of overstorey proteas. As a conservative estimate, any fire regime which do not allow for; (i) at the lower end, the second flowering of the slowest growing overstorey proteoid shrub in a community (second flowering because seed of most proteoid shrubs need ± 1 year to mature after flowering) and; (ii) at the upper end, the year before the fastest growing overstorey proteoid shrub become senescent in the community, will not maintain the species richness of fynbos communities. Any fire regime between these two extremes will be acceptable to maintain the species richness of any fynbos community. Temporal variability in the density of overstorey proteas may enhance the species richness of a community but, once this guild of species have been eliminated from an area, they are slow to

return (Bond 1988). The repeated absence of overstorey proteas may not only reduce the species richness of a community, but also result in an increase in the relative abundance of sprouters. High densities of understorey sprouters may affect hydrological processes in fynbos vegetation (Bosch *et al* 1986), indicating that the repeated absence of overstorey proteas also affect water runoff from mountain fynbos areas.

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APPENDIX 1: Frequency of species in 100 m² quadrats at Study Site 1 and 2. (Frequency values indicate presence of a species in 30 quadrats at Study site 1 and in 20 quadrats in Study Site 2. FB1 = Fire break 1; FB2 = Fire break 2; MATF = Mature fynbos; OLDF = Old fynbos.)

	SITE 1	SITE 2			
SPECIES		FB 2	MATF	FB 1	OLDF
Acrolophia lamellata	00	00	02	00	01
Agathosma capensis	21	20	16	20	20
Agathosma mundii	00	00	04	00	00
Agrostis bergiana	02	00	00	00	00
Alepidea cf. capensis	00	03	00	00	00
Anthospermum aethiopicum	14	00	00	00	00
Anthospermum ciliare	15	19	20	13	14
Aristea racemosa	19	00	00	00	00
Aristea zeyheri	00	00	03	00	07
Aspalathus aciphylla	00	06	00	01	07
Aspalathus rubens	17	16	00	08	08
Aspalathus shawii	02	00	00	00	00
Athanasia pachycephala	11	00	00	00	00
Berkheya cruciata	02	00	01	00	00
Brunia nodiflora	00	00	02	13	06
Caesia contorta	30	20	17	20	20
Cannamois scirpoides	25	18	19	20	20
Cannamois virgata	29	00	00	00	00
Centella virgata	29	07	06	04	12
Chrysocoma valida	00	00	01	01	08
Cliffortia falcata	30	00	00	00	00

SPECIES	SITE 1	FB 2	MATF	FB 1	OLDF
Clutia polifolia	00	00	00	18	08
Corymbium africanum	23	00	00	00	01
Corymbium glabrum	01	20	20	20	20
Cyclopia intermedia	00	10	08	17	13
Dianthus laingsburgensis	07	08	05	02	06
Disperago cf. ericoides	30	00	00	00	00
Dolichothrix ericoides	10	00	00	00	00
Drimia cf. elata	00	00	00	03	00
Ehrharta bulbosa	19	15	18	03	11
Ehrharta calycina	01	00	00	00	00
Ehrharta capensis	02	00	00	00	00
Ehrharta ottonis	08	01	05	01	02
Ehrharta ramosa	13	00	00	00	00
Elegia filacea	00	00	15	00	00
Elegia juncea	00	00	02	00	00
Elytropappus adpressus	02	05	16	13	11
Elytropappus gnaphaloides	28	01	07	03	12
Eragrostis capensis	00	17	13	13	20
Erica cerinthoides	00	11	03	20	13
Erica melanthera	19	00	00	00	00
Erica speciosa	11	00	00	00	00
Felicia filifolia	00	00	00	00	01
Ficinia deusta	30	00	03	00	03
Ficinia filiformis	30	20	20	20	20
Ficinia petrophylla	02	01	18	00	02

SPECIES	SITE 1	FB 2	MATF	FB 1	OLDF
Gazania krebsiana	00	05	01	08	03
Gladiolus floribundus	00	02	00	00	00
Gladiolus inflatus	00	00	00	00	01
Helichrysum anomalum	00	00	00	01	02
Helichrysum cymosum	00	00	00	00	01
Helichrysum felinum	00	00	00	00	01
Helichrysum rotundifolium	09	01	08	05	04
Helichrysum zwartbergense	25	06	13	06	20
Heliophila sp.	27	00	00	00	00
Hermannia flammea	00	01	00	00	01
Hesperantha pilosa	02	00	00	00	00
Hibiscus pusillus	01	00	00	00	00
Hypodiscus albo-aristatus	30	05	13	02	13
Hypodiscus striatus	12	20	20	20	20
Hypodiscus synchroolepis	07	00	00	00	00
Indigofera heterophylla	28	01	00	00	04
Indigofera sulcata	00	00	00	00	13
Ischyrolepis capensis	00	20	20	20	20
Ischyrolepis gaudichaudian	00	00	16	00	00
Ischyrolepis sieberi	21	00	00	00	00
Lampranthus scaber	00	18	16	15	17
Leucadendron barkeri	00	00	00	04	00
Leucadendron salignum	03	20	09	20	17
Lightfootia diffusa	00	19	02	10	15
Lightfootia rigida	00	00	01	00	01

SPECIES	SITE 1	FB 2	MATF	FB 1	OLDF
Lightfootia rubens	30	20	18	20	20
Linum africanum	26	15	01	04	07
Liparia confusa	01	00	00	00	00
Lobelia coronopifolia	04	02	00	04	09
Lobostemon marlothii	00	07	00	08	05
Merxmuellera arundinacea	00	12	00	11	08
Metalasia acuta	00	00	01	00	03
Metalasia massonii	30	01	07	02	14
Metalasia pulcherrima	00	01	00	00	05
Metalasia pungens	00	00	02	00	00
Muraltia squarrosa	12	00	00	00	00
Nivenia binata	00	00	02	00	01
Osteospermum scariosum	18	02	00	03	04
Othonna parviflora	09	00	00	00	00
Othonna sp.	26	00	00	00	00
Oxalis pocockiae	00	11	14	02	05
Pelargonium fruticosum	00	00	00	00	01
Pelargonium myrhifolium	01	00	00	00	00
Pelargonium ovale	30	01	02	03	06
Pelargonium scabrum	00	00	00	00	02
Pelargonium tricolor	00	01	00	00	00
Pentameris distichophylla	25	16	19	20	20
Pentameris macrocalycina	00	15	20	20	20
Pentaschistis aurea	23	00	00	00	00
Pentaschistis pallida	30	17	20	13	20

SPECIES	SITE 1	FB 2	MATF	FB 1	OLDF
Phylica imberbis	00	10	01	19	10
Phyllopodium elegans	30	00	00	00	00
Polygala garcinii	00	00	01	01	00
Protea canaliculata	00	00	00	00	01
Protea eximia	30	01	09	00	07
Protea lorifolia	08	15	20	06	20
Protea repens	28	14	20	11	20
Pteronia stricta	10	00	01	00	00
Rafnia capensis	01	00	00	00	00
Rafnia fastigiata	00	06	00	13	01
Rafnia zwartbergensis	19	01	00	08	01
Relhania calycina	00	19	04	19	13
Restio triticeus	30	20	20	20	20
Rhodocoma fruticosa	30	20	19	20	12
Romulea atrandra	25	00	00	00	00
Schizodium inflexum	01	00	00	00	00
Selago albida	30	16	20	16	20
Selago corymbosa	00	00	00	00	01
Senecio juniperinus	00	00	00	00	01
Senecio paniculatus	24	00	02	02	04
Senecio sp.	00	00	00	00	02
Senecio umbellatus	25	00	00	00	08
Stoebe aethiopica	00	05	05	03	08
Stoebe burchellii	00	00	00	00	01
Stoebe plumosa	00	00	00	01	00

SPECIES	SITE 1	FB 2	MATF	FB 1	OLDF
Stoebe spiralis	00	19	20	17	06
Struthiola dodecandra	19	00	00	00	00
Syncarpha canescens	00	01	10	00	01
Syncarpha ferruginea	11	02	03	02	02
Syncarpha milleflora	00	19	17	19	20
Syncarpha paniculata	21	19	20	11	15
Tetraria capillacea	02	00	05	00	00
Tetraria cuspidata	00	20	20	20	20
Tetraria sp. nov.	30	20	16	19	20
Tetraria ustulata	30	18	20	20	20
Thamnochortus rigidus	28	13	17	19	17
Themeda triandra	00	06	00	07	04
Theilera guthriei	07	00	00	00	00
Thesium carinatum	26	20	14	18	19
Thesium strictum	09	00	02	06	02
Thesium virgatum	00	04	00	02	02
Thoracosperma marlothii	01	14	20	00	00
Tritoniopsis antholyza	30	20	20	20	20
Ursinea anthemoides	30	01	02	05	02
Watsonia marlothii	07	00	00	00	00
Willdenowia teres	05	20	20	20	20

APPENDIX 2: Frequency of species in 0.25 m² quadrats, located in different post-fire micro-habitats, at Study Site 1. (Frequency values indicate presence of a species in 30 quadrats. "UNDER PROTEA" = quadrats located under burned canopies of 13-year old proteoid shrubs; "IN OPEN" = quadrats located in open with no proteoid overstorey in previous fire-cycle and < 25% sprouter basal cover; "IN SPROUTER" = quadrats located where sprouters had ≥ 80% basal cover in post-fire environment.)

SPECIES	UNDER PROTEA	IN OPEN	IN SPROUTER
Agathosma capensis	11	11	10
Anthospermum ciliare	05	05	00
Aristea racemosa	01	04	05
Aspalathus rubens	05	03	00
Berkheya cruciata	01	00	00
Caesia contorta	12	13	05
Cannamois scirpoides	01	00	01
Centella affinis	18	16	11
Cliffortia falcata	16	14	04
Ehrharta bulbosa	03	01	03
Elegia vaginulata	00	01	00
Erica cerinthoides	01	00	00
Erica speciosa	01	01	01
Erica umbelliflora	00	01	00
Ficinia deusta	16	09	06
Ficinia filiformis	24	21	06
Ficinia petrophylla	02	01	01
Helichrysum zwartbergense	01	02	00
Heliophila elongata	06	06	02

SPECIES	UNDER PROTEA	IN OPEN	IN SPROUTER
Hypodiscus albo-aristatus	19	21	02
Hypodiscus striatus	05	09	01
Indigofera heterophylla	14	09	02
Ischyrolepis capensis	00	01	00
Lightfootia diffusa	01	01	00
Lightfootia rigida	00	02	00
Linum africanum	04	02	00
Lobelia coronopifolia	01	01	00
Metalasia massonii	16	10	03
Muraltia squarrosa	02	00	00
Osteospermum scariosum	04	02	01
Othonna parviflora	01	01	00
Othonna sp.	01	01	00
Pelargonium myrrifolium	00	01	00
Pelargonium ovale	20	13	02
Pentameris distichophylla	13	12	03
Pentameris macrocalycina	15	10	11
Pentaschistis pallida	05	05	01
Phyllopodium elegans	25	22	14
Polygala garcinii	12	08	01
Protea eximia	10	09	01
Protea lorifolia	02	03	00
Protea repens	05	02	01
Pteronia stricta	01	03	01
Restio triticeus	17	14	03

SPECIES	UNDER PROTEA	IN OPEN	IN SPROUTER
Rhodocoma fruticosa	19	20	17
Romulea atrandra	09	08	02
Romulea fibrosa	01	01	00
Selago albida	06	05	01
Senecio paniculatus	04	02	00
Stoebe spiralis	12	09	03
Syncarpha paniculata	01	00	00
Tetraria cuspidata	11	11	04
Tetraria ustulata	07	02	30
Thamnochortus rigidus	02	02	01
Theilera guthriei	01	00	00
Thesium carinatum	02	05	00
Tritoniopsis antholyza	02	05	02
Ursinea anthemoides	27	25	09